ACTA BOTANICA

A QUARTERLY OF THE HUNGARIAN ACADEMY OF SCIENCES

Acta Botanica publishes original reports on botanical subjects in English, French, German, Spanish and Russian

Acta Botanica is published in yearly volumes of four issues by

AKADÉMIAI KIADÓ
Publishing House of the Hungarian Academy of Sciences
H-1054 Budapest, Alkotmány u. 21.

Manuscripts and editorial correspondence should be addressed to
Acta Botanica 1363 Budapest P.O. Box 24

Subscription information

Orders should be addressed to

KULTURA Foreign Trading Company
1389 Budapest P.O. Box 149

or to its representatives abroad

Acta Botanica Hungarica is abstracted/indexed in Biological Abstracts, Chemical Abstracts, Current Contents–Agriculture, Biology and Environmental Sciences, Excerpta Botanica, Excerpta Medica

© Akadémiai Kiadó, Budapest

INSTRUCTIONS TO AUTHORS

Papers will be considered for publication in *Acta Botanica Hungarica* only if they have not previously been published or submitted for publication elsewhere. They may be written in English, French, German, Russian or Spanish. From Hungarian authors papers are also accepted n Hungarian.

Manuscripts should be sent to

Prof. Pál Jakucs	or to	Prof. Attila Borhidi
editor-in-chief		managing editor
Ecological Department, Kossuth Lajos University, H-4010 Debrecen		Botanical Institute of the Hungarian Academy of Sciences H-2163 Vácrátót

Form of manuscript

Manuscripts should be typewritten in duplicate, double-spaced, 25 lines with 50 letters on each page. Articles should in general not exceed 25 typed pages tables and illustrations included. Acceptance depends on the opinion of one or more referees and the decision of the Editorial Board. Papers accepted for publication are subjected to editorial revision.

ACTA BOTANICA HUNGARICA

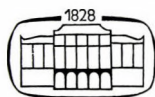
EDITORIAL BOARD

P. JAKUCS, Chairman

A. BORHIDI, G. FEKETE, L. FRIDVALSZKY,
P. JUHÁSZ-NAGY, M. KEDVES,
I. MÁTHÉ, T. PÓCS, I. PRÉCSÉNYI, T. SIMON, B. ZÓLYOMI

MANAGING EDITOR

A. BORHIDI

VOLUME 33 NOS 1—4

AKADÉMIAI KIADÓ, BUDAPEST

1987

ACTA BOT. HUNG.

ACTA BOTANICA

33/1—4 1987

CONTENTS

BOOK REVIEWS

CONTENTS

Acta Botanica Hungarica 33 (1–2), pp. 3–18 (1987)

COENOTONE, ECOTONE AND THEIR ROLE IN PRESERVING RELIC SPECIES

B. Zólyomi

INSTITUTE OF ECOLOGY AND BOTANY, HUNGARIAN ACADEMY OF SCIENCES, VÁCRÁTÓT, HUNGARY

(Received: 10 October 1986)

The meaning of ecotone has been reinterpreted by introducing the term coenotone. The analysis of ecological indicator values (T, W, R) for communities from the mountains of Hungary, as well as from the Hungarian Plain and Transylvania, proves that coenotone and ecotone are of great importance in preserving relic species.

The conditions of survival of relic species have always been an attractive research topic in ecology. Hypotheses and speculative statements can be very easily generated, as the applicability of objective research methods is considerably limited owing to temporal and historical factors. Nevertheless, ecologists must do their best to justify the assumptions from as many viewpoints as possible.

A possibility is a detailed coenotic analysis in the habitat of the species in question, i.e. a community study. The analysis of the geographical distribution of the species composing the community and a coenogenetic evaluation should also be attempted. The proof will usually be indirect; only in specific circumstances can direct evidence be provided (e.g. micro- and macrofossils in case of relic species of peat bogs).

Autecology and synecology may reveal the ecological behaviour of the relic species. Detailed syndynamic studies of relic species are very scarce, however. An ecological-dynamical approach to this problem may use the ecotone concept (see below).

The coenotic analysis of rock grasslands and steppe meadows of Transylvania led to the following conclusions (Zólyomi 1939, footnote on page 40):

"Auffallend ist die Erscheinung, daß die Reliktarten oft nicht in vollentwickelten Individuen bestimmter Assoziationen, sondern in Initialphasen oder Übergangsindividuen bzw. Übergangsassoziationen zu finden sind. Das heißt, an solchen Standorten, wo die Konkurrenzkraft der dominanten Arten der Assoziationen herabgesetzt ist. Z. B.: *Allium obliquum* kommt nur in Initialstadium der Übergangsassoziation *Avenastretum decori* vor (Aufn. 6). *Dracocephalum austriacum*: in der Tordaer-Schlucht in einer *Melica ciliata* — Fazies der genannten Assoziation (Aufn. 4) und bei Brassó in einem *Caricetum humilis*, welches Anklänge zum *Avenastretum* aufweist (Aufn. 1–2), ferner in Mittelungarn im Bükkgebirge in einen Übergangsindividuum des *Festucetum glaucae* zum *Caricetum humilis* und endlich in den Randgebieten der Ungarischen Tiefebene bei Kistápé (Komit. Tolna) wiederum in einem Übergangsindividuum zwischen dem *Festucetum sulcatae* und dem *Festucetum vaginatae*."

Then, the rules recognized were also found to apply to the survival conditions of glacial relics of the Central Range of Transdanubia (ZÓLYOMI 1950: 46). At that time, the central European phytosociologists did not know, or at least did not use, the term ecotone, which was defined by American and English ecologists (CLEMENTS 1928, WEAVER and CLEMENTS 1938, TANSLEY 1940, ODUM 1971, etc.). There is no doubt, however, that implicit reference is made to ecotone in the above example.

Ecotone is the transition between two, sometimes more, contrasting communities or habitats, for example, the forest margin between a steppe and a forest community. This zone is composed of a mixture of species from both communities and those occurring almost exclusively in this transitional part. The number of species and the density of some populations are often higher in the ecotone than in the neighbouring communities themselves.

The term ecotone is not restricted to long and narrow strips on the border of two communities; more extensive and well-separated transitional stands (associations, sub-associations, such as karstic beechwoods, *Fageto-Ornetum*, see below) may also be considered ecotones. They are analyzed by means of transects or linear samples taken perpendicular to the boundary line. Such studies have been performed in Hungary as well. The first intensive study of this kind was concerned with the alkali forest steppe at the edge of Hortobágy at Újszentmargita. Regarding one of three transects used in the gradient study it was established that "In der 'ecotone' der natürlichen Waldgrenze der Alkalisteppe gegenüber ist es 1966 gelungen, *Quercus pubescens* im Margitaer Wald aufzufinden". This is an isolated, relic occurrence (ZÓLYOMI and TALLÓS 1967: 60, MÁTHÉ et al. 1967: 74–76, ZÓLYOMI et al. 1972, 1974). In the Balaton Upland and the Vértes Mountains, mosaics of xerotherm forests, forest margins and grasslands ("Biogruppe") have been analyzed in detail by modern gradient analysis (JAKUCS 1972). Although the term ecotone is not used, this publication is properly cited as one providing an example for ecotone (WESTHOFF and VAN DER MAAREL 1978).

On the other hand, Dutch researchers dealt with the accurate interpretation as counter-like-terms of the ecotone and ecocline (VAN LEEUWEN 1960) and with the distinction of five theoretical boundary types (VAN DER MAAREL 1976). In this context we also refer to the "Rinteln" Symposium (1968, 1970 and VAN DER MAAREL 1974, FRESCO 1972). Recently as a case study, the boundaries of the annual grassland and coastal sage scrubs of Southern California, creating the so-called differencial profiles, have been studied by multivariate statistical analysis (TWINSPAN) (HOBBS 1986). By this way also five boundary types, but already factual ones were characterized (A—C ecotones, D—E ecolines).

On our part (FEKETE and ZÓLYOMI) we think that the concept of ecotone should be subjected to a partial re-interpretation so that it should become

adequate to the present day, modern synbiology and its purposeful division (synphenobiology, ecology).

After so many years, it seems unavoidable to reinterpret TANSLEY's and CLEMENTS' ecotone concept (FEKETE and ZÓLYOMI ined.) and consider it as being adequate to the recent subdivision of synbiology into synphenobiology and ecology. On the analogy of the useful terms of coenocline-ecocline (cf. JUHÁSZ-NAGY 1985), we could call coenotone the visible and physiognomically often clear-cut phenomena, and use the term ecotone (sensu stricto) for the causal background responsible for the coenotone. Since the phenomenon of coenotone can be described by coenological methods, the description should primarily be based on the changes of interspecific relationships, especially species-abundance changes and, consequently, diversity changes. In characterizing ecotone (sensu stricto), methods for the description of niche get into the focus: (a) niche breadth changes of populations, (b) niche overlaps for several populations and, in particular, the niche structure of a stand ('species packing').

In the study of ecotone, instrumental measurements yield most of the data, whereas in case of the coenotone emphasis is laid on a comparative coenotic analysis of vegetation. The latter facilitates the recognition of underlying factors based on the bioindication of species, stands and the whole plant community (see the application of W and R gradients below).

Returning to the example presented in 1939, I show a possibility to further development. The T—W—R bioindication system provides a more straightforward approach (ZÓLYOMI and PRÉCSÉNYI 1964, ZÓLYOMI et al. 1967). For all the species of the communities mentioned above, the indicator values for water economy (W) and soil reaction (R) were determined. The means of these values were obtained for each relevé, yielding an arrangement of communities in the coordinate system with W and R as axes. The occurrence of relic species is indicated by special symbols (Figs 1 and 2). The coenotone and ecotone position of *Dracocephalum austriacum* is thus indirectly justified ecologically. Data for comparison with the Kistápé relevés (JÁVORKA and ZÓLYOMI 1939–1940) were derived from a study of the sand vegetation of Szentendre-Island (ZSOLT 1943, see also PRÉCSÉNYI 1980).

The role of coenotone and ecotone in preserving relic species is most obvious in a unique, transitional association, the mixed karstic forest (*Fago-Ornetum*, ZÓLYOMI 1950, 1958) of the Triassic dolomite of Transdanubia in Hungary. This phytocoenosis has a peculiar species composition and is found on steep dolomite slopes of northern exposition. It is intermediate between the karstic shrubwood (*Cotino-Quercetum*) plus karstic oakwoods (*Orno-Quercetum*) of warmer and dryer microclimate and the beechwoods (*Laureolo-Fagetum*) of cool and wet microclimate. It is established that the karstic beechwood devel-

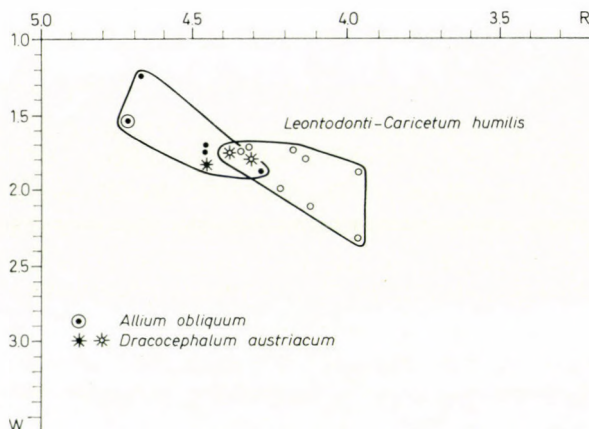



Fig. 1. Of the relic species of Transylvania, ***Allium obliquum*** from central Asia is in a pioneer, initial phase (the nearest isolated occurrence is in southern Ural, and it is distributed from the Tien Shan to the Lake Baikal area). ***Dracocephalum austriacum*** is of a transitional, coenotone and ecotone position. Explanation (for the other figures as well): W = water economy indicator value (0–10), R = soil reaction indicator value (1–5). Areas outlined correspond to the habitat of communities based on the mean W and R values

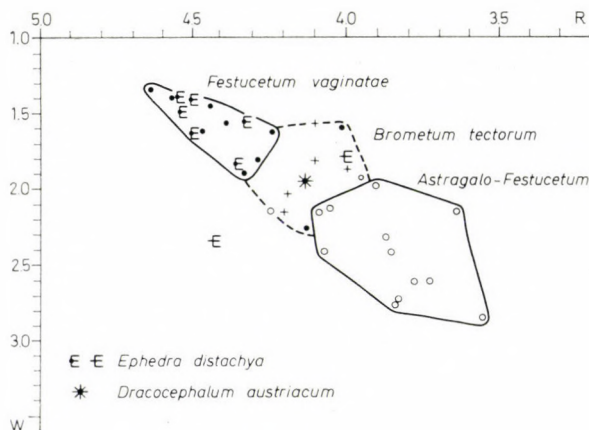



Fig. 2. ***Dracocephalum austriacum*** is in transitional, coenotone and ecotone position even in the localities of the Hungarian Great Plain, between the open sand grassland (***Festucetum vaginatae***) and the closed sand steppe (***Astragalo-Festucetum hirsutae***). On the contrary, ***Ephedra distachya*** appears to be a pioneer species. — Based on the position of ***Brometum tectorum***, it can only be a secondary pioneer, mainly a degraded stage

oped after the reforestation of the closed dolomite rock grassland (*Festuco-Brometum*) after the Ice Age.

Here, the species are exposed to the abrupt change of ecological conditions. Of the transitional zone the loose canopy (60–80%) and the dwarfishness of beech (8–16 m) are characteristic (see Fig. 4). The almost completely

closed carpet of the bromegrass community (*Festuco-Brometum*) is loosened by shading and the competition by the shallow-rooted beech. In this situation, the relic species are not eliminated owing to competition. During the climatic changes in long periods of the development of vegetation, the relic species might have survived in small areas without migration; in certain habitat patches microclimate provided the conditions for survival of these populations.

In the W—R coordinate system, not only the karstic beech stands are shown. Using my 120 relevés and other published and unpublished data (Jakucs and Fekete 50, Majer 33, Debreczy 28, Fekete 18, Borhidi and Isépy 9, Szőcs 9, Csapody 5), the complete ecological, and partly successional series of the dolomite vegetation of the Central Transdanubian Mts. have been established. There are two series corresponding to the southern and the northern slope vegetation (see Figs 3 and 4). The maximum elevation in the mountains is about 750 m a.s.l., and the dolomite areas do not exceed 550 m. The communities analyzed here are mainly found in deep valleys at an even lower elevation.

After the general notes, more concrete examples are to be discussed. On the southern slope, *Linum dolomiticum* is the most famous interglacial relic species of the starting stage of the series, the open dolomite grassland (*Seseleo-Festucetum pallentis*). Its occurrence is shown in Fig. 3. The ecotone position of this community towards the closed dolomite grassland (*Festuco-Brometum*) is topologically obvious. The abundant occurrence of *Linum dolomiticum* in transitional stands has been proved by statistical methods (Draskovits 1967). In the Budai–Pilis Mts. there is another relic species, *Thlaspi montanum*, represented by a single patch. The coenological analysis indicates the transitional position of this patch between the closed and the open dolomite grassland. On the dolomite of northern Bakony Mts., *Stipa bromoides*, a Mediterranean species, is an isolated preglacial relic. It survived in the *Cotino-Quercetum fagetosum* community (Fekete 1959, 1966) which is transitional between the karstic shrubwood and karstic beechwood. The coenotone and ecotone positions of this species are also illustrated in Fig. 3.

Another characteristic species of the open dolomite grassland (*Seseleo leucospermi-Festucetum pallentis*) is the endemic preglacial relic, *Seseli leucospermum*. Contrary to the previous species, it is a pioneer rather than a species in a coenotone-ecotone position (not shown in the Fig. 3, since this species is present in 27 stands of the 30 studied).

The starting plant community of the successional series of northern dolomite slopes is the closed dolomite grassland (*Festuco-Brometum*). During the s ecular succession after the Ice Age, this sub-mediterranean association developed from subalpine limestone grasslands with *Sesleria*. However, some characteristic elements of the sub-alpine rock grasslands have been survived as glacial relics (Fig. 4).

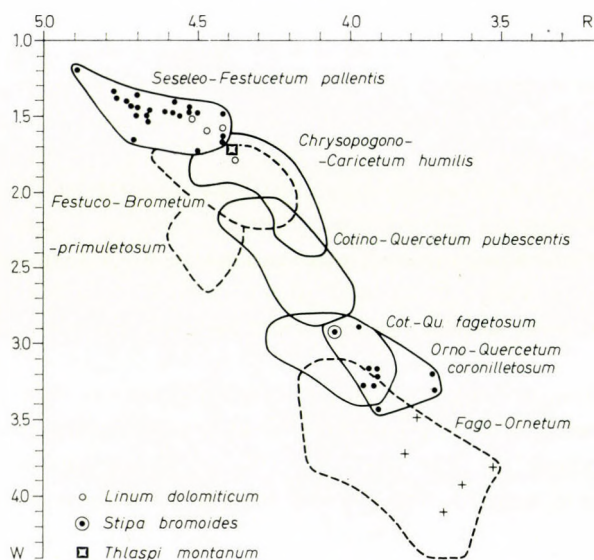



Fig. 3. Ecological, and partly successional, series of the communities on the southern dolomite slopes of Transdanubian Range. Dotted line envelops the adjacent communities of the northern slope + signifies the stands of *Fago-Ornetum* found only in S exposition in the northern Bakony Mts. The coenotone and ecotone position of relic species included is self-explanatory. The series of communities may exemplify coenocline and ecocline

Fig. 4. In the *Fago-Ornetum* the beech grows to a dwarf form, ramified in the waistheight (Photo: FELFÖLDY 1950)

The most famous example is **Primula auricula.** Its survival under the changed macroclimatic conditions was possible in two habitat types. The first is the initial stage of the community mentioned above, which developed on steep, northern-northeastern cliffs with poor plant cover, where competition among species was negligible. The other, more rare, possibility is offered by the transitional zone between *Festuco-Brometum* and the karstic beechwood (*Fago-Ornetum festucetosum amethystinae*) and by the forest margin. The latter case has been studied by transect analysis (Isépy 1970, 1978).* At the orographic timberline there is an abrupt change of ecological conditions. Two topographically adjacent communities appear in the field, whereas there is a wide gap between them in the topological diagram (W 2.40 → 3.70).

The extinction of *Sesleria* from most of the Transdanubian Mts. is a complex phenomenon, a result of migration, competition, adaptation and genetic factors, and needs further investigations. *Carduus glaucus* is a glacial relic shared by the closed dolomite grassland and the karstic beechwood. This is a denominative species of the sub-alpine *Sesleria* rock grassland in the Tátra Mts., but in the mountains of Transdanubia it is more protected and therefore more abundant in the karstic beechwoods than in the rock grassland. *Festuca amethystina* is a glacial relic found only in *Fago-Ornetum.* Characteristic relic species are *Calamagrostis varia* and *Carex alba*, which are hardly found in other associations. The primary role of coenotone and ecotone in preserving relic species is well-established in case of *Fago-Ornetum.*

Another sub-association of karstic beechwoods is *Fago-Ornetum caricetosum albae.* This represents a transitional stage towards the *Mercuriali-Tilietum* scree forest and the commonest type of beechwoods (*Laureolo-Fagetum*). *Allium victorialis* is a noted glacial and boreal relic on the border of this coenotone community. The diagram of Fig. 5 indicates its occurrence only in the Burok-valley, but the situation is the same in the Esztergáli-valley (Vida, in Fekete et al. 1961) and, 200 km to the northwest, in the Ablakoskő-valley of the Bükk Mts. (Zólyomi et al. 1954, 1955). The relevés taken from topographically adjacent stands on the border of two associations are positioned far apart in the topological gradient diagram. This indicates a sudden change especially along the W gradient (W 4.3–4.7).

In addition to the W—R diagram of the ecological, and partly successional, series of northern dolomite slopes, a profile diagram was drawn to facilitate comprehension of the situation (Fig. 6). Owing to the special geomorphology, some special habitats (Sonder-Standort) developed. Therefore, some associations of the series became permanently established in a steady state. In the development of soil, strong erosion is compensated for by signif-

* Unfortunately, the point made in my former reports on the relic species (Zólyomi 1939, 1950) escaped Isépy's attention. His general statements, therefore, appear as being never recognized in earlier vegetation studies.

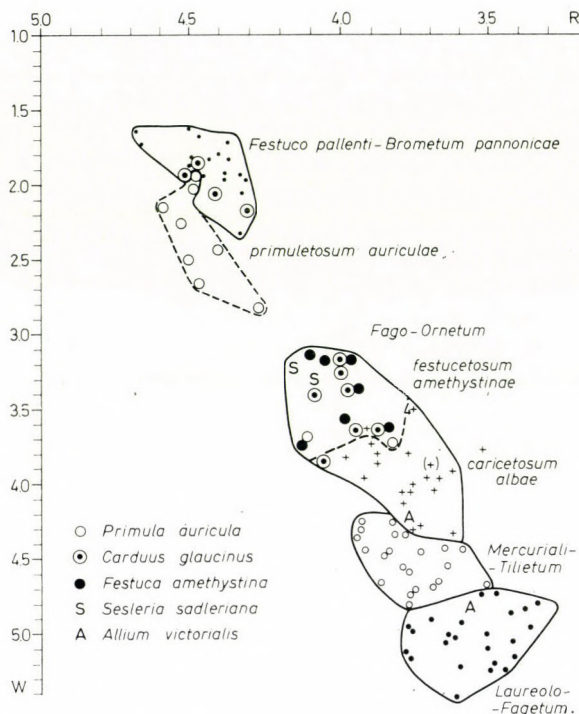



Fig. 5. **Ecological, and partly successional, series of communities on the northern dolomite slopes of the Transdanubian Range. The outstanding relic-preserving role of *Fago-Ornetum*, a transitional ecotone and coenotone community, is illustrated**

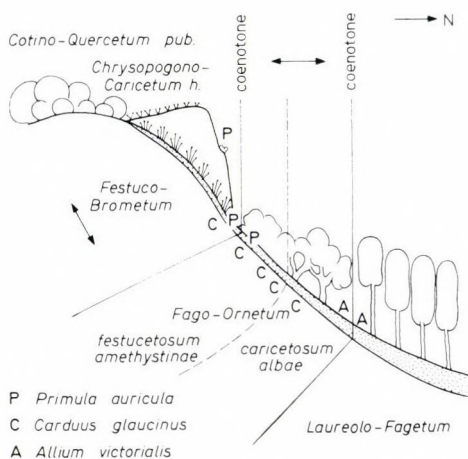



Fig. 6. **Profile diagram showing the topography and vegetation of the northern dolomite slopes of the Transdanubian Range**

icant accumulation of materials. Major change, either progressive or regressive, only occurred during the secular succession, and it can be expected in the future. The type of secular succession is a penetrating one rather than transgression. This offers another possibility for the survival of relics.

Regarding the full series, the increase and a subsequent decrease in the coenotone and ecotone are illustrated in Table 1.

Table 1

Number of species and cases

Associations	Number of			Mean No. of species per relevé
	relevés	species	cases	
Festuco-Brometum primuletosum	(6)	87	208	35
Festuco-Brometum pannonici	(25)	137	933	37
Fago-Ornetum festucetosum amethystinae	(15)	196	949	61
Fago-Ornetum caricetosum albae	(15)	189	847	55
Mercuriali-Tilietum	(20)	146	634	32
Laureolo-Fagetum	(25)	140	592	30

The European yew (*Taxus baccata*) is a popular tree in the parks of Hungary. It is otherwise a native species occurring only at Szentgál, Bakony Mts., where it is abundant, and in a few patches in the Bükk Mts. It is doubtful whether this species actually survived here the last glacial period. I pointed out earlier (Zólyomi 1950, 1954) its postglacial relic character and its association with the karstic beechwood and the *Sesleria* beechwood. A monograph of the yew forests at Szentgál is due to Majer (1978). Based on his data and my relevés, the occurrences of yew in Hungary are illustrated in the W—R coordinate system (Fig. 7). The yew-dominated forests of Bakony Mts. are the result of intensive forest exploitation, the thinning of closed beech stands, and are thus considered derived types.

The original ecological optimum of yew might have been in the transition between the karstic forest, the scree forest and the typical beechwoods. Although the stands examined are too few to obtain acceptable frequency values, a rough approximation by frequency curves is shown in the W—R coordinate system in order to illustrate the application of W—R values. For sufficient "n", the values are more precise, and the ecological optimum of species may also be determined in the indicator value system.

Considering the whole successional and ecological series on dolomite, the method seems applicable to characterize numerically the ecological behaviour of species, so that subjective comparisons are replaced by objective assessment.

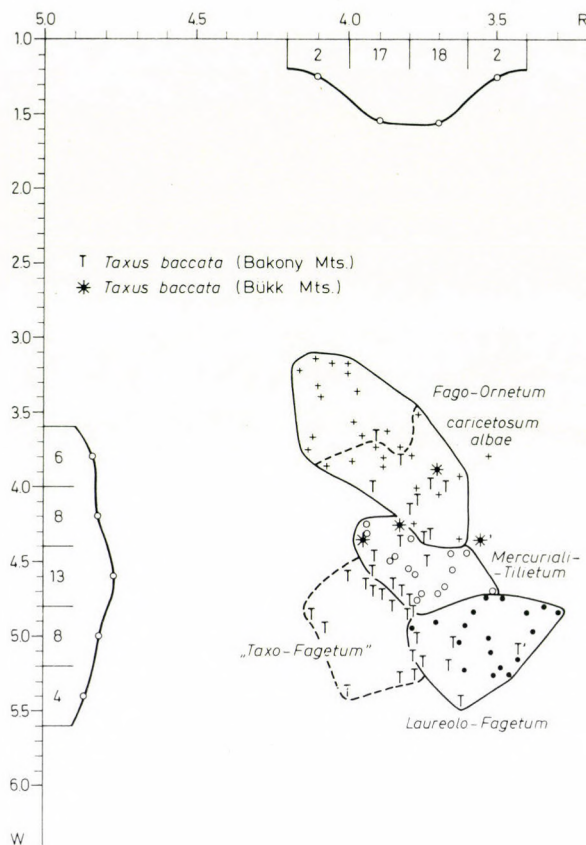



Fig. 7. Relic occurrences of *Taxus baccata* in Hungary according to the W and R indicator values. Explanations of symbols: T: Szentgál, Bakony Mts., T': Borostyánhegy, Bakony Mts., +: Dolomite of Sebes-víz, Bükk Mts. (*Seslerio-hungaricae-Fagetum*), Szinva-valley (*Mercuriali-Tilietum*)

In addition to the W and R values, other indicators, such as temperature (T) and light (L) may also be used.

The coenotone and ecotone communities significantly increase the chance of species for hybridization. Species differing in ecological requirements may co-occur here. Examples are *Sorbus aria* of the cool and wet montane region and *S. torminalis* of the collin xerotherm oakwoods, which meet in *Fago-Ornetum*, the karstic beechwood of dolomite. A wide variety of hybridogenous agamospecies developed on the dolomits of Transdanubian Mts.: *Sorbus semi-incisa* (Budai Mts.), *S. vértesensis* and *S. pseudovértesensis* (Vértes Mts.), *S. rédliana* and *S. bakonyensis* (Bakony Mts.), and *S. balatonica* and *S. gayeriana* (Keszthely Mts.). In the same place occur together *Mercurialis perennis*, a species of the hornbeam-beechwood, and *M. ovata* from the karstic shrub-

Table 2

Fago-Ornetum

Synthetic phytosociological table

a) subass. *festucetosum amethystinae* (15 relevés)
b) subass. *caricetosum albae* (15 relevés)

Layer (A–C)	Phytosociological group species		Constancy (K I–V) and abundance-dominance value (AD 1–5) (a)		(b)		Presence in relevés (group percentages) (a)		(b)	
	Orno-Cotinion, Orno-Cotinetalia									
A	*Fraxinus ornus*		2—3	V	+—3	V	15		14	
B	*Fraxinus ornus*		1—2	V	1—2	V	14		12	
B	*Sorbus cretica*		+	II	+	I	6		2	
B	*Cotinus coggygria*		1—2	I	—2	I	2		3	
B	*Cotoneaster tomentosa*		+	II	+	I	6		1	
B	*Amelanchier ovalis*		+	I	.		1		.	
							44		32	
								4.6%		3.8%
C	*Oryzopsis virescens*		+—3	II	+—2	III	8		4	
C	*Mercurialis ovata*	D	+—1	II	.		5		.	
C	*Mercurialis ovata* × *perennis*		+—1	II	+—2	I	5		3	
C	*Coronilla emerus*	D	1—2	II	.		5		.	
C	*Coronilla coronata*		+—1	I	+—1	I	2		3	
C	*Tamus communis*		+	I	.		2		.	
							27		10	
								2.8%		1.2%
	Quercetalia, Quercetea pubescenti-petraeae									
AB	*Sorbus aria* × *torminalis* (6 agamospecies)		+—2	IV	+—1	III	15		12	
B	*Cornus mas*		+—2	IV	+—2	III	12		9	
B	*Euonymus verrucosa*		+—1	IV	+—1	IV	12		12	
B	*Viburnum lantana*		+—2	IV	+—1	IV	10		12	
B	*Berberis vulgaris*		+	IV	+	III	12		9	
AB	*Sorbus torminalis*	D	+—1	II	+—2	IV	9		14	
AB	*Quercus pubescens*	D	+—2	III	+—2	I	9		2	
B	*Pyrus pyraster*		+	II	+	I	5		2	
	other sp. (a: 5, b: 5)			I		I	(6)		(9)	
							90		81	
								9.5%		9.6%
C	*Chrysanthemum corymbosum*		+—1	V	+—1	V	13		13	
C	*Galium mollugo*		+—1	V	+—2	III	13		9	
C	*Teucrium chamaedrys*	D	+—2	V	+—1	III	13		7	
C	*Polygonatum odoratum*	D	+—2	V	+—2	III	14		9	
C	*Primula canescens*	D	+—2	V	+—2	III	14		9	
C	*Melittis grandiflora*		+—1	IV	+—1	IV	10		10	
C	*Vincetoxicum hirundinaria*	D	+—1	V	+	II	14		6	
C	*Laserpitium latifolium*		+—2	IV	+—2	III	10		9	
C	*Erysimum odoratum*	D	+	IV	+	II	11		6	
C	*Brachypodium pinnatum*		+—2	III	1—2	II	9		4	
C	*Arabis hirsuta*		+	III	+	II	8		5	
C	*Arabis turrita*		+	III	+—1	III	7		8	
C	*Cytisus nigricans*		+—1	III	+	II	8		6	
C	*Hypericum montanum*		+	III	+	II	8		4	
C	*Peucedanum cervaria*		+—1	III	+	II	7		4	

Table 2 (Continued)

Layer (A–C)	Phytosociological group species		Constancy (K I–V) and abundance-dominance value (AD 1–5) (a)	(b)	Presnce in relevés (group percentages) (a)	(b)
C	*Ranunculus polyanthemos*	D	+ III	+ I	7	2
C	*Serratula tinctoria*	D	+—1 III	+ I	7	2
C	*Valeriana offic. v. collina*	D	+—2 III	+ I	7	3
C	*Calamintha clinopodium*		+ I	+ III	3	8
C	*Coronilla varia*		+ I	+—1 III	3	8
C	*Bupleurum falcatum*		+—2 II	+—2 II	4	5
C	*Clematis recta*		+—(2) II	+ I	6	1
C	*Silene nutans*		+ II	+ II	4	5
C	*Viola hirta*		+ I	+ II	3	6
	other sp. (a: 23, b: 25)		I—II	I—II	(44)	(53)
					247	202
					26.0%	23.8%
	Locally characteristic species (relic sp., p.p. *Erico-Pinion*)					
AB	*Taxus baccata*	D	.	2—3 I	.	3
C	*Carex alba*		1—4 III	3—4 V	9	15
C	*Calamagrostis varia*	D	1—4 IV	1—2 I	11	3
C	*Festuca amethystina*	D	1—4 III	.	7	.
C	*Allium victorialis*		.	2—4 I	.	1
C	*Knautia kitaibelii* ssp. *tomentella* (destr.)		x	.	x	.
					27	22
					2.8%	2.6%
	Relic species (*Seslerietalia*)					
C	*Biscutella laevigata*	D	+ IV	+ I	11	2
C	*Polygala amara*	D	+ IV	—1 I	10	1
C	*Phyteuma orbiculare*	D	+—1 III	+—1 I	7	3
C	*Galium pumilum austriacum*		+—1 II	—1 I	4	1
C	*Carduus glaucinus*		+—3 II	1 I	6	1
C	*Leontodon incanus*		+ I	.	3	.
C	*Coronilla vaginalis*		+ I	.	2	.
C	*Primula auricula* ssp. *hungarica*		+ I	.	1	.
C	*Sesleria sadleriana*		0—2 I	.	2	.
C	*Anthyllis vuln.* ssp. *alpestris*		+ I	.	2	.
C	*Daphne cneorum* (*Erico-Pinion*)		+ I	.	2	.
					50	8
					5.3%	0.9%
	Festuco-Brometea (incl. *Brometalia*, *Festuco-Bromion*)					
C	*Anthericum ramosum*	D	+—2 V	+—2 III	14	7
C	*Carex humilis*	D	1—3 V	2 I	14	1
C	*Campanula rotundifolia*	D	+—1 V	+—1 I	13	2
C	*Leucanthemum margaritae*	D	+—1 V	+—1 II	13	6
C	*Pimpinella saxifraga*		+—1 IV	+ II	10	6
C	*Bromus erectus*	D	+—2 IV	.	10	.
C	*Asperula tinctoria*	D	+—1 III	+ I	9	1
C	*Hieracium cymosum*	D	+—1 III	+ I	8	1
C	*Inula ensifolia*	D	+—1 III	+ I	7	2
C	*Stachys recta*		+ II	+ I	5	2
	other sp. (a: 25, b: 12)		I—II	I	(49)	(22)
					152	50
					16.0%	5.9%

Table 2 (Continued)

Layer (A–C)	Phytosociological group species		Constancy (K I–V) and abundance-dominance value (AD 1–5) (a)		(b)		Presence in relevés (group percentages) (a)		(b)	
	Fagetalia, Carpino-Fagetea (incl. *Cephalanthero-Fagion, Fagion illyricum*)									
A	*Fagus silvatica*		2—4	IV	3—5	V	12		15	
B	*Fagus silvatica*		+—1	IV	+—1	IV	10		10	
A	*Acer platanoides*		+—1	II	+—2	III	4		8	
B	*Acer platanoides*		+—1	II	+	I	5		2	
AB	*Tilia platyphyllos-caucasica-pseudorubra*		+—3	II	+—2	II	5		5	
AB	*Tilia cordata*		+—1	II	+	II	6		4	
AB	*Sorbus aria*		+	I	+	II	1		5	
AB	*Acer pseudoplatanus*		+	I	+	I	2		1	
							45	4.7%	50	5.9%
C	*Carex digitata*		+—1	IV	1	IV	10		11	
C	*Euphorbia amygdaloides*	D	+—1	II	+—1	IV	4		10	
C	*Lathyrus vernus*	D	.		+—1	IV	.		11	
C	*Lilium martagon*		+	II	+	III	6		9	
C	*Mercurialis perennis*	D	+	I	+—2	III	3		7	
C	*Viola mirabilis*	D	+—1	I	+—2	III	2		7	
C	*Asarum europaeum*		+	I	+	II	2		6	
C	*Aquilegia vulgaris*		+—1	II	—1	I	5		2	
C	*Bupleurum longifolium*		+—1	I	+—2	I	2		2	
C	*Cephalanthera damasonium*		.		+	II	.		4	
C	*Cephalanthera rubra*		+	I	+	I	1		1	
C	*Daphne laureola*		.		+—1	I	.		3	
C	*Primula vulgaris*		+	I	+—1	II	1		4	
C	*Dentaria enneaphyllos*		+	I	+	I	1		1	
	other sp. (a: 9, b: 12)			I		I	(14)		(18)	
							51	5.4%	96	11.3%
	Querco-Fagea									
AB	*Quercus petraea*		—1	II	2	II	4		4	
BC	*Hedera helix*		+—1	III	+—2	IV	8		11	
B	*Crataegus oxyacantha*		+	II	+	III	5		5	
B	*Cornus sanguinea*		+—2	II	+—1	II	5		6	
B	*Corylus avellana*		+—2	II	+	II	5		6	
B	*Staphylea pinnata*		+—3	II	+—3	II	5		6	
B	*Acer campestre*		+—2	I	+—2	II	3		6	
B	*Clematis vitalba*		+	II	+	II	4		5	
B	*Juniperus communis*		+—1	II	.		5		.	
	other sp. (a: 5, b: 5)			I		I	(12)		(10)	
							56	5.9%	62	7.3%
C	*Solidago virga-aurea*		+—1	IV	+—2	V	10		14	
C	*Campanula persicifolia*		+—1	IV	+—1	IV	12		12	
C	*Campanula rapunculoides*		+—2	III	+—2	V	9		15	
C	*Convallaria majalis*		+—1	III	+—3	IV	7		10	
C	*Hieracium silvaticum*		+—1	III	+—2	IV	9		10	
C	*Veronica chamaedrys*	D	+	II	+	IV	4		10	

Table 2 (Continued)

Layer (A–C)	Phytosociological group species		Constancy (K I–V) and abundance-dominance value (AD 1–5) (a)		Constancy (K I–V) and abundance-dominance value (AD 1–5) (b)		Presence in relevés (group percentages) (a)		Presence in relevés (group percentages) (b)	
C	*Ajuga reptans*	D	+	I	+—2	IV	3		11	
C	*Digitalis grandiflora*		+—1	III	+	II	8		4	
C	*Asplenium linnaei*		+	II	+—1	III	6		8	
C	*Brachypodium silvaticum*		+—1	II	+—2	III	6		8	
C	*Epipactis helleborine*	D	+	I	+	III	2		7	
C	*Fragaria vesca*		+	II	+	III	6		8	
C	*Galium silvaticum*	D	+—1	I	+—2	III	3		8	
C	*Melica uniflora*	D	+	I	+—2	III	2		8	
C	*Melica nutans*		+—1	II	+	III	5		7	
C	*Poa nemoralis*	D	+	I	+—2	III	3		7	
C	*Hieracium sabaudum*	D	+	I	+—2	III	2		8	
C	*Veratrum nigrum*		+—1	II	+—2	I	6		3	
	other sp. (a: 8, b: 11)			I—II		I—II	(20)		(18)	
							123	13.0%	175	20.7%
	Indifference									
C	*Cardaminopsis arenosa*		+—2	III	+—2	IV	9		11	
C	*Dactylis polygama*		+—1	IV	+—2	IV	11		12	
C	*Euphorbia cyparissias*		+	III	+	III	8		8	
C	*Polypodium vulgare*		+	I	+	II	2		5	
	other sp. (a: 6, b: 12)			I		I—II	(7)		(23)	
							37	3.9%	59	7.0%
					Total of presence:		949		847	
	Total of species:		196		189			99.9%		100.0%

D = differential species.

Date of the relevés: 1947—1949 published at first in ZÓLYOMI, B. (1950): Acta Biol. Acad. Sci. Hung 1: 38—46, 66.

Localities of the relevés: Budai Mts. (10 relevés), Vértes and South-Bakony (10 relevés), North-Bakony Mts. (5 relevés), Balaton-Highland (5 relevés).

wood. In the karstic beechwood, some populations are composed of hybrids (*M. paxii*) or transitional forms (*M. longistipes*) (see ZÓLYOMI 1950, p. 46). The dynamical study of the ecological and successional series of dolomite vegetation has been continued (e.g. the diversity studies by PRÉCSÉNYI from 1984).

The term ecotone and the associated problems (such as the coenotone) have been largely overlooked, especially in European coenological studies. Now we witness an apparent rediscovery of these concepts. According to the most recent news, a new project ("Ecotone project") will be launched within the framework of SCOPE (Special Committee of Problem of Environment).

In this paper the significance of coenotone and ecotone was only emphasized from the viewpoint of relic species. Their importance in general aspects of coenology and ecology is obviously greater. For problems arising from the application of ecological indicator values, it is worth performing time-consuming and more expensive instrumental ecotone measurements. Then, these surveys may reveal more precisely the casual background that characterizes the coenotone.

REFERENCES

Clements, F. E. (1928): *Plant Succession and Indication.* 2nd ed. Washington.

Debreczy, Zs. (1966): Die xerothermen Rasen der Péter- und Tamás-Berge bei Balatonarács. *Annales Mus. Nat. Hung.* **58:** 223–241.

Debreczy, Zs. (1968): Der Flaumeichen-Hochwald (Orno-Quercetum pannonicum) des Balaton-Oberlandes. *Acta Botanica Acad. Sci. Hung.* **14:** 261–280.

Draskovits, R., Kovács-Láng, E. (1968): Mikroklimamessungen in Kalkstein- und Dolomitfelsenrasen. *Annales Univ. Sci. Budapest, Sect. Biol.* **9–10:** 115–129.

Ellenberg, H. (1979): *Zeigerwerte der Gefässpflanzen Mitteleuropas.* 2nd ed. Scripta Geobotanica, pp. 122.

Fekete, G. (1959): *Stipa bromoides* (L.) Dörfl., eine neuentdeckte Pflanze in Ungarn. *Acta Botanica Acad. Sci. Hung.* **5:** 349–356.

Fekete, G. (1966): Der xerotherme Flaumeichen-Buschwald des nördlichen Bakony-Gebirges. *Annales Hist. Nat. Mus. Nat. Hung.* (Pars Botanica) **58:** 207–221.

Fekete, G. (1985): A terresztris vegetáció szukcessziója: elméletek, modellek, valóság. In *A cönológiai szukcesszió kérdései,* Ed. Fekete, G. Biológiai Tanulmányok **12.** Akadémiai Kiadó, Budapest, 31–63.

Fekete, G., Járai-Komlódi, M. (1962): Die Schuttabhangwälder der Gerecse- und Bakony-Gebirges. *Annales Univ. Sci. Budapest, Sect. Biol.* **5:** 115–129.

Fekete, G., Majer, A., Tallós, P., Vida, G., Zólyomi, B. (1961): Angaben und Bemerkungen zur Flora und zur Pflanzen-Geographie des Bakonygebirges. *Annales Hist. Nat. Mus. Nat. Hung.* (Pars Botanica) **53:** 241–253.

Fresco, L. F. M. (1972): A direct quantitative analysis of vegetational boundaries and gradients. In: E. van der Maarel, T. Tüxen (eds): *Grundfragen und Methoden in der Pflanzensoziologie.* Ber. Intern. Symp. Rinteln 1970, Den Haag, pp. 99–111.

Hobbs, E. R. (1986): Characterizing the boundary between California annual grassland and coastal sage scrub with differential profiles. *Vegetatio 65:* 115–126.

Isépy, I. (1968): Schlucht- und Schuttabhangwälder im Vértes-Gebirge (ung. mit deutsche Zusammenfassung). *Bot. Közlem.* **55:** 199–204.

Isépy, I. (1970): Phytozönologische Untersuchungen und Vegetationskartierung im südöstlichen Vértes-Gebirge. *Acta Botanica Acad. Sci. Hung.* **16:** 59–110.

Isépy, I. (1978): Dauerquadrat-Untersuchungen in Pflanzengesellschaften mit alpinen und montanen Reliktpflanzen im Transdanubischen Mittelgebirge (Ungarn). *Vegetatio* **37:** 187–189.

Jakucs, P. (1961): *Die phytocoenologischen Verhältnisse der Flaumeichen-Buschwälder Südostmitteleuropas.* Akadémiai Kiadó, Budapest, 314 pp.

Jakucs, P. (1972): *Dynamische Verbindung der Wälder und Rasen.* Akadémiai Kiadó, Budapest, pp. 228.

Juhász-Nagy, P. (1984): *Beszélgetések az ökológiáról.* Mezőgazdasági Kiadó, Budapest, 235 pp.

Juhász-Nagy, P. (1985): Bevezetés a szündinamikába. In *A cönológiai szukcesszió kérdései.* Ed. Fekete, G. Biol. Tanulm. **12:** 13–30.

Majer, A. (1978): *A Bakony Tiszafása.* Akadémiai Kiadó, Budapest.

Majer A. (1981): Der Eibenreiche Buchenwald von Bakony-Szentgál. *Acta Botanica Acad. Sci. Hung.* **27:** 53–103.

Máthé, I., Zólyomi, B., Précsényi I., Kovács, M. (1967): Der Alkali-Waldsteppenwald von Margita als Arbeitsgebiet im IBP. *Guide der Exkursionen des Internationalen Geobotanischen Symposiums.* Eger–Vácrátót. Ed.: Zólyomi, B. MTA KESZ, Budapest, Gradientenuntersuchungen: pp. 74–76.

Mészáros-Draskovits, R. (1967): Zönologische Verhältnisse von *Linum dolomiticum* Borb. *Bot. Közlem.* **54:** 193–201.
Mészáros, I., Jakucs, P., Précsényi, I. (1981): Diversity and niche changes of shrub species within forest margin. — *Acta Bot. Acad. Sci. Hung.* **27:** 421–437.
Odum, E. P. (1971): *Fundamentals of Ecology.* Saunders, Philadelphia–London–Toronto. 6. Ecotones and the concept of edge effect. pp. 157–159.
Précsényi, I. (1981): Changes in the diversity of the vegetation during succession. *Acta Botanica Acad. Sci. Hung.* **27:** 189–198.
Szőcs, Z. (1971): Die Buchenwälder des Vértesgebirges. I. *Annales Univ. Sci. Budapest,* **13:** 253–268.
Tansley, A. Q. (1940): *The British Islands and Their Vegetation.* I. pp. 215.
Van Leeuwen, C. G. (1966): A relation theoretical approach to pattern and process in vegetation. *Wentia* **15:** 25–46.
Van der Maarel, E. (1974): Small-scale vegetational boundaries; on their analysis and typology. In: W. H. Sommer, R. Tüxen (eds): *Tatsachen und Probleme der Grenzen in der Vegetation* Ber. Symp. Intern. Ver. Vegetationskunde. Rinzeln 1968, J. Cramer, Lehre. pp. 75–80.
Van der Maarel, E. (1976): On the establishment of plant community boundaries. *Ber. Deutsch. Bot. Ges.* **89:** 415–443.
Weaver, J. E., Clements, F. E. (1938): *Plant Ecology.* 2nd ed. McGraw-Hill, N.Y.–London, pp. 601.
Westhoff, V., van der Maarel, E. (1980): The Braun-Blanquet approach. In: Whittaker, R. H. (ed.): *Classification of Plant Communities.* 2nd ed. Junk, The Hague, pp. 287–399.
Zólyomi, B. (1939): Felsenvegetationsstudien in Siebenbürgen und im Banat. *Ann. Mus. Nat. Hung.* (Pars Botanica), footnote No. 40.
Zólyomi, B. (1942): Die Mitteldonau-Florenscheide und das Dolomitphänomen. — *Bot. Közlem.* **39:** 209–231.
Zólyomi, B. (1950): Fitocenozi i lesomelioracii obnazhenii gor Budü (Les phytocoenoses des montagnes de Buda et le reboisement des endroits dénudés). *Acta Biol. Acad. Sci. Hung.* **1:** 7–67.
Zólyomi, B. (1958): Budapest és környékének természetes növénytakarója (The natural vegetation of Budapest and its environs). In: *Budapest Természeti Képe.* Ed.: Pécsi, M. Akadémiai Kiadó, Budapest, pp. 509–642.
Zólyomi, B. (1964): Methode zur ökologischen Charakterisierung der Vegetationseinheiten und zum Vergleich der Standorte. Précsényi, I.: Mathematisch-statistische Bearbeitung der Beispiele. *Acta Bot. Acad. Sci. Hung.* **10:** 377–416.
Zólyomi, B., Baráth, Z., Fekete, G., Jakucs, P., Kárpáti, I. V., Kovács, M., Máthé, I. (1966–1967): Einreihung von 1400 Arten der ungarischen Flora in ökologische Gruppen nach TWR-Zahlen. *Fragmenta Bot. Mus. Hist. Nat. Hung.* **4:** 101–142.
Zólyomi, B., Jakucs, P., Baráth, Z., Horánszky, A. (1955): Forstwirtschaftliche Ergebnisse der pflanzengeographischen Kartierung im Bükkgebirge. *Acta Botanica Acad. Sci. Hung.* **1:** 361–395. In ungarischer Sprache schon 1954 — *Az Erdő,* pp. 78–82, 97–105, 160–171.
Zólyomi, B., Máthé, I., Précsényi, I., Szőcs, Z. (1974): Productivity of vegetation in the IBP experimental area at Újszentmargita. *Acta Botanica Acad. Sci. Hung.* **20:** 193–203. First in Hungarian (1972): *MTA Biol. Oszt. Közlem.* **15:** 31–43.
Zólyomi, B., Tallós, P. (1967): Galatello-Quercetum roboris. In: *Guide der Exkursionen des Internationalen Geobotanischen Symposiums.* Eger–Vácrátót. Ed.: Zólyomi, B. pp. 88.
Zsolt, J. (1943): A Szentendrei sziget növénytakarója (The vegetation of the Szentendre Island). *Index Horti Botanici Univ. Budapest* **6:** 1–19.

Acta Botanica Hungarica 33 (1–2), pp. 19–40 (1987)

FACIES AND THEIR RESPONSE TO PERTURBATION IN A TURKEY OAK – SESSILE OAK WOOD

G. Fekete[1], Klára Virágh[1] and A. Horánszky[2]

[1] RESEARCH INSTITUTE FOR ECOLOGY AND BOTANY, HUNGARIAN ACADEMY OF SCIENCES, VÁCRÁTÓT, HUNGARY

[2] DEPARTMENT OF PLANT TAXONOMY AND ECOLOGY, L. EÖTVÖS UNIVERSITY, BUDAPEST, HUNGARY

(Received: 1 April 1986)

This paper is concerned with the coenological status of the variants of an oakwood community and examines whether their separation from one another is similar in magnitude. The understorey facies of the zonal oakwood *Quercetum petraeae-cerris* in Hungary were evaluated to determine (1) the intra-facies similarity, which reflects how the community is co-ordinated, (2) the inter-facies segregation, and (3) the resistance against perturbation and forest weeds. The ordination and classification of facies were based on different resemblance coefficients, using either presence/absence or abundance/dominance scores. There was a very slight discontinuity among the "common" facies in the presence/absence case. Whenever the dominance of a single species was the most influential factor, the use of quantitative indices facilitated the recognition of inter-facies segregation. The separation of rare (edaphic) facies was quite different. For example, the *Luzula* facies exhibited a high intra-facies uniformity even in the presence/absence situation, and its segregation from the others was also striking. The effect of perturbation was unequivocal, the facies became either much poorer or richer in species. High intra-facies similarity in the *Luzula* facies was associated with a resistence to species invasion.

Introduction

I. A common and important property of plant communities is their tendency to form related variants even within the same geographical region. This is especially true for communities composed of several physiognomically distinct layers. Forests are obvious examples. Related variants of beechwoods are known all over Europe, these are named after the dominant species of the herb layer (*Asperula odorata*, *Mercurialis perennis*, *Oxalis acetosella*, etc.), just like those of spruce forests (e.g. *Hylocomium*, *Vaccinium myrtillus*, *Sphagnum* spp.). There are many more examples listed in any "Synopsis" or "Conspectus" written by followers of the Zürich–Montpellier approach. This indicates, of course, that the dominance of some species often, but not necessarily, influences the whole floristic composition, so that these variants may correspond to a syntaxonomic rank (e.g. association, subassociation, consociation, etc.). The variants usually share a large group of species, these (or more precisely, the constant and the so-called characteristic species) represent the basis for the description of associations. The associations are "codified" by a consensus among leading synoptic syntaxonomists. The application of associations is still useful although they are more or less of symbolic significance, since only the variants are manifested in Nature. In vegetation mapping, at a sufficiently small scale, the variants are recognized and registered, rather than the associations. Also, a statement as "the beechwoods have good mushroom production" is misleading, since we know well that only the *Luzula* facies of beechwoods has this capability.

A natural question arises: if there are several "attempts" in Nature to manifest a community, what is the success of each? Are the variants equally "well-organized" or, alter-

natively, are some of them in fact less "perfect" ? Such intuitive and perhaps pointless questions are commonly asked under the influence of evidence often reported in the coenological literature. There are some groups of such evidence.

The first group includes indirect evidence derived from the comparison of observations on many communities. They eventually suggest some compositional uncertainty. According to these types of evidence (1) the tolerance of variants is certainly different. This is supported by the fact that some variants are present in climatically and geologically different areas, whereas others are not. Thus, quoting the beechwood example again, the "*Asperula* beechwood" seems more tolerant than a "*Fagetum altherbosum*". Evidences are also available suggesting that (2) the composition of variants changes over the regions. An example at a large scale is that *Asperula* beechwoods occur in the atlantic, the central European as well as in the Balkan regions, but these are quite different in species composition. It is also true that (3) this compositional change differs with the variants. (4) Whereas some variants are easily recognized in region A (and their separation is confirmed by analytical results), their distinctness diminishes in region B. For example, in the northern part of the mountain range in Hungary, the variants of beechwoods, characterized by the dominance of *Asperula* and *Oxalis*, separate quite well in space, they have wide spatial extension and indicate different habitat properties. However, in the western part of these mountains, variants are no longer distinguishable and, consequently, they cannot be mapped. (In addition to our personal observations, one is referred to Zólyomi, Jakucs, Baráth and Horánszky 1955 and Magyar 1933.) Probably these problems are related to zonality. The phenomena described above have not been examined exhaustively, and especially the background factors have been neglected [regarding (4), for instance, some rearrangements and comprimations seem likely in the niche space].

The other group of evidence is related to dynamic properties such as vulnerability and stability. Sylvicultural practice (forest management and forest cultivation) and forest science provide many useful examples. When the foresters "discovered" phytocoenology for themselves and subsequently developed the ideas of forest typology, they realized that alternative variants of a community (forest types) require different management strategies. The problem of cyclic regeneration is especially relevant to our study. It is known that in some forest types after complete deforestation, a very crude intervention that is comparable only to catastrophes in natural communities, the spontaneous regeneration processes restore almost deterministically the former species composition. Other forest types, however, require careful management if the purpose is the maintenance of former species composition. Again, the beechwoods serve as a good example. Danszky and Rott (1964) give substantial information on the Hungarian aspects of this topic.

II. Let us consider the other large group of deciduous forests, the oakwoods. In the hilly areas and lower mountains of Hungary, the dominant type is the turkey oak—sessile oak wood, which covered 19% of the area of the country before deforestation (cf. Jakucs 1980). The name of the community, *Quercetum petraeae-cerris*,* is straight to the point, both species have good yield in the community. In fact, turkey oak, which is a Balkan species, reaches its optimum growth in this wood. The community is zonal and develops usually on deep brown forest soils. Extensive stands are found especially in the Northern Mountain Range. It seems reasonable to compare the two extreme examples. In the section Buda Mts.–

* In addition to the central European *Quercus petraea*, the related *Qu. dalechampii* and, more sporadically, *Qu. polycarpa* may also form stands. These species are distributed in the Balkan and in the Balkan and Asia Minor, respectively. In the understorey, European, Eurasiatic, Pannonian and north Balkan species dominate. This floristic picture corresponds with the fact that *Quercetum petraeae-cerris* has a transitional position between the subcontinental-Sarmatic *Potentillo-Quercetum* and the Balkan *Quercetum farnetto-cerris* (Soó 1963).

Zemplén Mts. of the range there are several ecological gradients, from the dry and warm plains to the cool and wet Carpathian foothills.

The turkey oak — sessile oak woods in the Buda Mts., in the close vicinity of Budapest, have the same species composition and variants that are usually encountered in the dry and warm Pannonian hilly areas. ZÓLYOMI, who recognized and first described this community, reports on three variants (*Festuca heterophylla*, *Poa nemoralis* and *Melica uniflora* oakwoods, ZÓLYOMI 1950, 1958). It is noted that in the *Melica uniflora* variant 6–8 species of hornbeam-oak woods reach higher frequency (in the herb and shrub layer). Turkey oak and sessile oak are dominant in all variants.

On the northern edge of the range, in the Zemplén Mts., the *Quercetum petraeae-cerris* community also develops. Its composition is demonstrated by the tables of SIMON (1977). Owing to the closeness of the Carpathian Mts., the vitality of mesophilous woods (hornbeam-oak woods, beechwoods) strongly influences the extension, variants and composition of turkey oak — sessile oak woods. If the Buda Mts. stands are taken as a standard, even though such a choice is arbitrary and therefore controversial, the following comparison can be made. *Quercus cerris* retreats from the communities in the Zemplén Mts.; it is absent, in fact, from the whole area of the mountains. In addition to the *Festuca heterophylla* and *Poa nemoralis* variants, a *Luzula nemorosa* facies ("forest type", SIMON 1977) occurs. The most striking difference is that hornbeam may show up in any variant. However, the habitats potentially dominated by *Melica uniflora* are occupied by hornbeam-oak wood, so that the *Melica* facies of turkey oak-sessile oak community cannot develop anyway.

Thus, the compositional uncertainty of facies, exemplified by beechwoods, may also be documented for turkey oak — sessile oak woods. The large-scale zonality changes of vegetation influence not only the extension of the stands of a community but affect the development and relative importance of facies and, above all, their floristic composition.*

The examples given above motivated us to look for situations in which the facies may be analyzed objectively. For practical reasons (see below) the turkey oak — sessile oak woods were selected for study. To facilitate comparison, stands within the same geographical region were considered.

Material

Turkey oak — sessile oak woods are especially well represented in the Szentendre-Visegrád Mts., at the Danube Bend (Pilis Landscape Protection Area, MAB Biosphere Reserve). This community extends over a large area in these mountains, where andesite is the main bedrock. (Other oakwoods, such as the xeromesophilous, submediterranean *Quercus pubescens* woods are smaller in extension if compared to the Transdanubian Mts., cf. HORÁNSZKY 1960.) For this reason, *Quercetum petraeae-cerris* has ample space to develop; it is shown by the altitude range of the community (200–600 m).

The variants of *Quercetum petraeae-cerris* are distinguished and named, with emphasis on the dominant species, based on the understorey vegetation. The variants, termed the facies,** indicate different habitats, since there is a relationship between the species composition of the understorey and growth of the tree level.

* For the turkey oak — sessile oak woods of the intermediate areas see also ZÓLYOMI et al. (1955) (Bükk Mts.), SZUJKÓ-LACZA (1964) (Börzsöny Mts.), KOVÁCS (1975) (Mátra Mts.) KOVÁCS and PODANI (1979) (Tarna Region, Mátra Mts.).

** Although some understorey types are given subassociation rank in the Hungarian tradition, we avoid the use of this rank. Also, the categories and terms used by central European coenologists are cited only for reference. The term facies is used here in a neutral sense, rather than in any coenotaxonomical context.

Table 1

Summarized phytosociological table with the species of high constancy values and the differential species of the facies

	Melica uniflora		*Poa nemoralis*		*Festuca heterophylla*		*Brachypodium pinnatum*		*Luzula albida*	
	facies									
	A—D	C	A—D	C	A—D	C	A—D	C	A—D	C
Astragalus glycyphyllos	+	IV	+	V	+	III		II	+	III
Anthericum ramosum	+—1	III		I	+	III	+	III	+—1	IV
Primula veris canescens		II	+—1	IV	+	IV	+	III	+—1	III
Trifolium alpestre		II	+	IV	+—1	V	+—2	IV	+—1	IV
Campanula rapunculoides	+—2	III	+—2	IV		II	+	III	—	—
Melittis grandiflora	+—1	IV		II	+	III	+—1	IV		II
Serratula tinctoria	+—3	III		II	+	III		II	+	III
Galium mollugo		I	+	III	+—1	III		II	+—1	IV
Digitalis grandiflora		II		I	+—1	IV	+—1	V	+	III
Hypericum perforatum		I		I	+	III	+—2	III	+	III
Phleum phleoides		I		I	+—1	III	+—2	III	+	III
Viscaria vulgaris		I		I	+—2	IV	+	IV	+	V
Geum urbanum	+	III	+	III		I	—	—	—	—
Viola cyanea	+—1	IV		II	+	III		I		I
Convallaria majalis	+—2	III	+	II		II	+—1	III		I
Lathyrus vernus	+	V		II		II	+	III		I
Genista tinctoria ssp. *elatior*		I	+—1	III	+—1	III		I		I
Origanum vulgare	—	—		I	+—1	III	+—1	IV		I
Silene nutans	—	—	+	III		II		II	+—2	V
Calamagrostis arundinacea		I	—	—		I	+	III	1—4	IV
Dactylis glomerata	+—3	III		I	—	—	—	—	—	—
Carex pilosa	+—3	V	—	—		I	—	—	—	—
Heracleum sphondylium	+	III	—	—	—	—	—	—	—	—
Rubus fruticosus s. l.	+	IV	—	—		I		I	—	—
Viola silvestris	+	III		I		I	—	—		I

Coronilla varia		I	+	III		II		II		I
Galium aparine		I	+—2	III		II	—	—	—	—
Lathyrus niger		II		II	+—1	IV		II	—	—
Inula hirta	—	—		II	+—1	III		I	—	—
Luzula campestris		I		I	+	III		II		I
Poa angustifolia		I		II	+—1	III		II	—	—
Sedum sexangulare	—	—	—	—	+	III		I		II
Cardaminopsis arenosa	—	—		II		I	+	IV		II
Cynanchum vincetoxicum		I		I		I	+	III	—	—
Cystopteris filix-fragilis	—	—		I		I	+—2	III		II
Brachypodium pinnatum	—	—	—	—		I	2—4	V	—	—
Hieracium sabaudum		I		II		II	+	III		II
Melampyrum nemorosum	—	—	—	—		I	+	III		II
Polygonatum odoratum		I		II		I	+—5	II		II
Stachys officinalis		I	—	—		II	+—1	III		II
Teucrium chamaedrys	—	—		I		II	+—2	IV		I
Valeriana officinalis		I		II		II	+—1	IV		II
Veratrum nigrum	—	—	—	—		I	+—1	III		I
Anthoxanthum odoratum		I		I	—	—	—	—	+—1	V
Chrysanthemum leucanthemum		II		I		II	—	—	+—1	V
Cytisus nigricans	—	—		I		II	—	—	+—1	III
Hieracium bauhini	—	—	—	—		II		I	+—1	III
Luzula albida		I		I		II		II	+—3	V
Veronica officinalis	—	—	—	—		I		I	+—1	IV

A—D: abundance—dominance values; C: constancy values

The facies described earlier by HORÁNSZKY (1964) from this area are as follows.

The *Melica uniflora* facies is the most fresh facies of the community and is bordered by hornbeam-oak woods. Still, we cannot state that this facies is exclusively found at the higher parts of the oakwood zone, since within that zone hornbeam-oak woods may develop anywhere if the physiographic conditions allow. Thus, the closeness of this facies to the hornbeam-oak woods is the most characteristic property. It is supported by the higher frequency of *Carpinus betulus* in the foliage and herb layer; in the latter even beech saplings may occur. Other *Querco-Carpinetum* species are also present in this facies (Table 1). No doubt that the *Melica* facies corresponds to the most favourable habitat, since this facies produces the highest timber volume. For *Quercus cerris* this facies represents a transitional position; climatic-mesoclimatic effects sometimes result in the full absence of this species (Frost traces often developing on the scattered trees refer to this fact). However, we should note that the proportion of turkey oak is primarily determined by forest management, i.e. an artificial factor, in all facies.

The *Festuca heterophylla* facies develops on flat terrains with deep soils. The roundish tufts of *Potentilla alba* and *Carex montana* are characteristic; later these tufts become ring-like. Sometimes, *Poa nemoralis* also appears in this facies. In spring, the melted snow is stagnant; it is a possible explanation for the occurrence of *Serratula tinctoria*, a species of boggy meadows. We could state that this facies is a typical, floristically rich turkey oak—sessile oak wood, which is never found in transitional situation. Although this is generally true, there are extrazonal stands of the *Festuca heterophylla* facies on dryer, steep, sometimes gravely slopes. However, in this case the flora is poorer than in stands on falt areas.

In fact, the *Poa nemoralis* facies, especially if thinning of woods creates favourable light conditions, can develop from any other facies. In addition, on steep slopes there are poorer stands that were dominated by *Poa nemoralis* originally. These are always neighboured by thermophilous oak woods or hornbeam-oak woods.

The *Brachypodium pinnatum* facies is confined to small areas, usually on steep slopes. The stands have low growth rate. According to the floristic composition, this facies is closest to the thermophilous oakwoods. Some species they share are: *Cardaminopsis arenosa, Cynanchum vincetoxicum, Polygonatum odoratum, Teucrium chamaedrys*, and *Veratrum nigrum.*

The *Luzula albida* facies is usually found in the neighbourhood of acidophilous oak woods. The closure of the foliage and shrub levels is the lowest, just like the growth rate. Some acidophilous-acidofrequent species often occur; and the presence of *Chrysanthemum leucanthemum*, a meadow species, is also striking.

According to frequency and distribution, two groups of facies can be distinguished: 1. *Melica uniflora, Festuca heterophylla* and *Poa nemoralis*, and 2. *Brachypodium pinnatum* and *Luzula albida*. Those in group 1 are common, widely spread facies, sometimes they can be considered as zonal. The other two facies are edaphic variants confined to small areas.

For a more general characterization, the facies are to be compared based on the so-called W and R indicator concept (ZÓLYOMI 1964). A short summary of this concept is given in Fig. 1 in which the facies are grouped according to water supply and soil reaction. The most fresh is the *Melica* facies, as it penetrates more than the others into the section corresponding to favourable water supply. Regarding water supply, the largest area in the diagram is occupied by the *Festuca heterophylla* facies. As to soil reaction, the *Poa nemoralis* and *Brachypodium* acies are shifted the farthest towards the basic reaction, whereas the *Luzula* facies occupies he opposite position, with a very poor water supply.

Several apparently undisturbed stands are to be found in the mountains. In addition, the floristic composition of more and more stands drastically changed in the past 10–15 years owing to perturbation.

Table 2

Phytosociological table (the numbers under each facies are the serial numbers of the sample quadrats)

	A									B							C					D						E					F			AA			BB						CC		
Name of the facies	*Melica* facies									*Poa* facies							*Festuca heterophylla* facies					*Brachypodium* facies						*Luzula* facies					*Festuca rupicola* facies			Degraded *Melica* facies			Degraded *Poa* facies						Degraded *Festuca heterophylla* facies		
Numbering of sample quadrats	1	2	3	4	5	34	39	42	47	6	7	8	9	10	35	41	11	12	13	14	15	16	17	18	19	20	40	21	22	23	24	25	26	27	28	36	38	37	30	33	43	44	45	46	29	31	32
Acer campestre	—	0.2	0.2	2.5	0.2	—	0.2	5	0.2	—	—	—	—	0.2	5	5	—	—	—	—	0.2	—	—	—	—	0.2	5	—	—	—	—	0.2	—	—	—	—	—	0.2	—	2	—	5	5	5	—	5	5
Acer platanoides	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Carpinus betulus	1.4	0.2	2.5	0.2	0.2	15	5	3	5	—	—	—	0.2	0.2	—	0.2	—	0.2	—	—	—	0.2	0.2	0.2	—	—	0.2	0.2	0.2	—	0.2	0.2	—	—	—	5	5	5	—	5	—	—	5	10	—	—	—
Cerasus avium	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	2	2	—	—	—	—	—	—	—	—	—	—
Cerasus mahaleb	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	5	5
Cornus mas	—	—	—	—	15	—	—	5	—	0.2	0.2	—	0.2	—	—	—	0.2	—	—	—	—	0.2	—	1.4	—	0.2	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cornus sanguinea	—	—	0.2	—	—	—	—	5	—	—	—	—	—	—	5	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	4	—	—	0.2	—	—	—	—
Corylus avellana	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—
Crataegus monogyna	—	0.2	9	1.4	—	5	5	5	—	0.2	0.2	0.2	—	—	—	—	—	2.5	—	—	—	—	—	—	0.2	—	5	—	—	—	—	0.2	—	0.2	—	—	5	5	9	2	5	5	—	15	—	5	5
Crataegus oxyacantha	0.2	—	15	62.5	0.2	5	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	5	—	—	0.2	—	—	—	—	5	—	5	5
Euonymus europaeus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
Euonymus verrucosus	—	—	—	—	0.2	2	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
Fagus silvatica	1.4	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—
Fraxinus excelsior	—	0.2	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	0.2	0.2	—	5	—
Fraxinus ornus	0.2	—	0.2	0.2	2.5	5	0.2	15	—	—	2.5	0.2	0.2	0.2	5	5	—	—	—	0.2	0.2	0.2	0.2	0.2	2.5	1.4	5	0.2	0.2	0.2	0.2	0.2	0.2	1.4	0.2	2	5	0.2	15	4	5	30	0.2	—	15	5	10
Ligustrum vulgare	—	—	—	0.2	—	3	5	5	—	—	—	—	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	2	—	5	9	5	—	—	—	0.2	—	5	5
Malus silvestris	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Populus alba	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
Prunus spinosa	—	—	—	0.2	0.2	2	0.2	0.2	—	0.2	—	0.2	—	—	—	5	—	1.4	—	—	—	—	—	—	—	—	—	—	—	15	—	—	0.2	0.2	—	5	—	—	—	—	0.2	0.2	—	—	—	5	5
Pyrus pyraster	—	—	—	—	—	—	0.2	5	0.2	0.2	—	—	—	0.2	5	5	—	0.2	—	—	—	0.2	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	2	2	—	—	1	—	5	—	5	—	—	—
Quercus cerris	—	0.2	37.5	2.5	—	80	35	35	5	0.2	—	—	—	37.5	25	15	—	37.5	—	—	—	—	15	0.2	—	—	—	—	0.2	—	—	—	—	62.5	0.2	35	5	30	50	80	40	45	5	65	50	5	30
Quercus petraea	37.5	87.5	62.5	62.5	62.5	10	35	45	70	62.5	87.5	87.5	87.5	15	60	50	62.5	37.5	37.5	87.5	37.5	37.5	15	87.5	37.5	37.5	65	62.5	87.5	37.5	37.5	62.5	87.5	37.5	87.5	45	75	50	55	10	40	10	80	5	55	50	30
Q. pubescens	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	—	—	50	40	30
Q. robur	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—
Rhamnus catharticus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	5	—	5	—
Ribes uva-crispa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rosa canina	—	—	0.2	0.2	0.2	—	—	5	0.2	0.2	—	0.2	—	—	—	0.2	—	0.2	—	0.2	—	—	0.2	0.2	—	—	0.2	—	—	—	—	0.2	0.2	—	—	—	—	—	0.2	2	—	5	0.2	3	0.2	5	5
Sorbus domestica	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—
S. torminalis	0.2	—	—	—	0.2	—	5	—	—	0.2	—	0.2	—	—	5	5	—	—	0.2	0.2	0.2	0.2	0.2	—	—	—	5	0.2	—	—	0.2	0.2	—	0.2	—	0.2	—	5	—	2	—	—	0.2	0.2	—	—	—
Tilia cordata	0.2	0.2	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.2	9	0.2	—	—	—	9	0.2	0.2	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	5
T. grandiflora	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T. platyphyllos	—	—	0.2	—	0.2	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—
Ulmus scabra	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5
Achillea collina	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. distans	2.5	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	0.2	—	2.5	1.4	—	9	0.2	0.2	2.5	0.2	0.2	0.2	—	—	0.2	—	—	—	—	—	—	—	—	0.2	0.2	—	0.2	—	—	0.2	—
Agropyron repens	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—
Agrostis tenuis	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ajuga genevensis	—	1.4	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	1.4	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	0.2
A. reptans	—	—	0.2	—	—	2	0.2	—	—	—	—	0.2	—	—	—	—	0.2	2.5	—	0.2	—	—	—	—	—	9	0.2	—	—	—	—	0.2	—	—	0.2	3	0.2	0.2	—	2	—	0.2	0.2	0.2	—	—	—
Alliaria petiolata	—	—	—	—	—	0.2	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0.2	—	—	—	—	—	—
Allium montanum	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. paniculatum	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	0.2	—	—	—	—	—	—
A. scorodoprasum	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	37.5	—	—	—	—	—	—	—	—	—	—	0.2	—	—
Alopecurus pratensis	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—
Anemone ranunculoides	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Table 2 (cont. — 2)

	A									B							C					D						E					F			AA			BB						CC		
Name of the facies	*Melica* facies									*Poa* facies							*Festuca heterophylla* facies					*Brachypodium* facies						*Luzula* facies					*Festuca rupicola* facies			Degraded *Melica* facies			Degraded *Poa* facies						Degraded *Festuca heterophylla* facies		
Numbering of sample quadrats	1	2	3	4	5	34	39	42	47	6	7	8	9	10	35	41	11	12	13	14	15	16	17	18	19	20	40	21	22	23	24	25	26	27	28	36	37	38	30	33	43	44	45	46	29	31	32
Anthemis tinctoria	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—
Anthericum ramosum	0.2	—	1.4	—	0.2	—	0.2	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	0.2	0.2	0.2	—	—	—	0.2	—	0.2	2.5	0.2	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—
Anthoxanthum odoratum	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.5	2.5	0.2	1.4	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—
Arabis hirsuta	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—
Arrhenatherum elatius	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	0.2	—	—	0.2	—	—	—	—	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Artemisia absithium	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Asarum europaeum	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Asperula glauca	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—
A. odorata	0.2	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	0.2	—	—	—	—
Asplenium trichomanes	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Astragalus glycyphyllos	0.2	0.2	0.2	0.2	—	—	0.2	0.2	—	0.2	0.2	0.2	0.2	0.2	0.2	—	0.2	0.2	0.2	—	0.2	—	0.2	0.2	—	—	—	0.2	0.2	—	—	0.2	0.2	0.2	—	—	—	—	0.2	—	—	2	0.2	—	0.2	0.2	0.2
Avenastrum pubescens	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Barbarea vulgaris	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Betonica officinalis	—	—	0.2	0.2	—	0.2	0.2	0.2	—	—	—	—	—	—	4	0.2	0.2	2.5	—	—	—	—	1.4	0.2	0.2	—	0.2	0.2	—	—	0.2	—	0.2	—	—	0.2	—	—	—	5	0.2	0.2	0.2	—	—	—	—
Brachypodium pinnatum	—	—	—	—	—	—	0.2	—	15	—	—	—	—	—	30	—	—	—	9	—	—	37.5	15	50	37.5	26	40	—	—	—	—	—	0.2	—	—	0.2	0.2	0.2	—	4	15	—	—	—	—	—	—
Brachypodium silvaticum	—	—	—	—	—	—	—	0.2	—	—	1.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	2.5	—	—	—	—	—	—	1	—	—	0.2	0.2	3	0.2	0.2	—
Briza media	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
Bromus ramosus ssp. *benekeni*	—	0.2	—	—	—	0.2	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	0.2	—	0.2	—	—	—	—
Calamagrostis arundinacea	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	0.2	—	—	0.2	50	15	2.5	26	2.5	—	—	—	65	70	50	—	0.2	0.2	—	—	—	—	—	—
Calamintha clinopodium	0.2	—	0.2	0.2	0.2	—	3	0.2	0.2	0.2	—	0.2	0.2	0.2	5	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	—	0.2	0.2	0.2	0.2	—	—	—	—	0.2	—	0.2	0.2	0.2	0.2	2	0.2	—	3	—	10	2	5
Campanula cervicaria	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C. glomerata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C. patula	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
C. persicifolia	0.2	0.2	—	—	0.2	5	—	—	0.2	0.2	—	—	0.2	2.5	—	0.2	0.2	0.2	2.5	0.2	0.2	0.2	0.2	0.2	—	—	0.2	0.2	2.5	0.2	0.2	0.2	0.2	0.2	0.2	0.2	—	0.2	0.2	1	0.2	0.2	0.2	—	0.2	—	0.2
C. rapunculoides	—	9	0.2	—	2.5	10	—	0.2	—	0.2	0.2	—	9	2.5	4	—	0.2	—	—	—	—	0.2	0.2	0.2	—	—	—	—	—	—	—	—	0.2	—	0.2	0.2	0.2	—	0.2	1	—	—	0.2	—	—	—	—
C. trachelium	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cardamine impatiens	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C. pratensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
Cardaminopsis arenosa	—	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	0.2	—	—	0.2	0.2	0.2	0.2	—	—	—	—	2.5	1.4	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—
Carex divulsa	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—
C. michelii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—	0.2	—	—	2	—	—
C. montana	2.5	—	9	—	—	0.2	—	—	—	—	—	—	—	9	0.2	3	—	2.5	—	—	—	—	—	—	—	0.2	0.2	—	0.2	—	—	0.2	0.2	—	—	—	—	—	—	—	5	—	—	—	—	10	—
C. muricata	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—
C. pairei	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	0.2	—	—	—	0.2	—	0.2	—	0.2	—	—	—	—
C. pilosa	37.5	0.2	0.2	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0.2	—	—	—	—	—	—
C. silvatica	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
C. tomentosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Carlina vulgaris	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—
Centaurea micranthos	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—
C. stenolepis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	0.2	—
Centaurium minus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
Cephalanthera damasonium	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	0.2	—	—	—
Cerastium vulgatum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chaerophyllum temulum	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chelidonium majus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—
Chrysanthemum corymbosum	0.2	—	1.4	0.2	0.2	3	0.2	5	0.2	2.5	0.2	—	2.5	1.4	8	5	—	15	0.2	2.5	—	1.4	0.2	2.5	0.2	0.2	3	0.2	1.4	0.2	1.4	0.2	0.2	—	0.2	4	0.2	0.2	—	2	0.2	0.2	0.2	—	0.2	—	—
C. leucanthemum	—	—	0.2	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	2.5	0.2	—	—	—	—	—	—	—	1.4	2.5	0.2	0.2	0.2	—	2.5	—	—	—	—	—	0.2	—	—	—	—	—	—	—
Circaea lutetiana	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—

Table 2 (cont. — 3)

	A									B							C					D						E					F			AA			BB						CC		
Name of the facies	*Melica* facies									*Poa* facies							*Festuca heterophylla* facies					*Brachypodium* facies						*Luzula* facies					*Festuca rupicola* facies			Degraded *Melica* facies			Degraded *Poa* facies						Degraded *Festuca heterophylla* facies		
Numbering of sample quadrats	1	2	3	4	5	34	39	42	47	6	7	8	9	10	35	41	11	12	13	14	15	16	17	18	19	20	40	21	22	23	24	25	26	27	28	36	37	38	30	33	43	44	45	46	29	31	32
Cirsium arvense	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
C. vulgare	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
Clematis vitalba	—	—	—	—	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Colchicum autumnale	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Convallaria majalis	—	—	15	—	0.2	—	—	2	0.2	—	—	—	0.2	—	3	—	0.2	0.2	—	—	—	—	2.5	0.2	—	1.4	0.2	0.2	—	—	—	0.2	0.2	—	—	3	3	0.2	—	2	—	—	0.2	—	—	—	—
Coronilla varia	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	0.2	0.2	—	0.2	—	—	0.2	—	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	2	0.2	—	0.2	0.2	0.2
Corysalis solida	—	0.2	—	—	—	—	—	—	—	—	—	2.5	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cruciata ciliata	0.2	—	0.2	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—	0.2	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
Cynanchum vincetoxicum	—	—	0.2	—	—	—	0.2	3	0.2	—	—	—	—	—	0.2	—	—	0.2	—	—	—	0.2	0.2	—	0.2	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	0.2	—	0.2	—	—	—	0.2
Cystopteris filix-fragilis	—	—	—	—	—	—	—	—	—	—	0.2	—	2.5	—	—	—	—	—	—	—	—	0.2	—	0.2	15	—	—	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cytisus nigricans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	2.5	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—
C. supinus incl. *aggregatus*	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—
Dactylis glomerata	—	2.5	—	—	0.2	3	0.2	3	5	—	2.5	1.4	—	0.2	3	0.2	—	9	9	1.4	0.2	—	—	0.2	15	0.2	0.2	0.2	0.2	—	—	0.2	—	0.2	0.2	0.2	—	0.2	0.2	1	5	0.2	3	0.2	0.2	—	—
Danaa cornubiensis	2.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dentaria bulbifera	—	0.2	0.2	37.5	0.2	—	—	—	—	—	—	9	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—
Seschampsia caespitosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—
Dianthus armeria	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	0.2	0.2	—
D. pontederae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dictamnus albus	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Digitalis grandiflora	—	—	1.4	—	0.2	—	0.2	3	0.2	—	0.2	—	—	—	0.2	—	0.2	2.5	—	1.4	0.2	1.4	1.4	0.2	0.2	0.2	4	1.4	1.4	0.2	1.4	—	—	0.2	0.2	—	0.2	—	—	—	—	0.2	0.2	—	—	—	—
Doronicum hungaricum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dryopteris filix-mas	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Epilobium montanum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
E. parviflorum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
E. roseum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
E. tetragonum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
Erigeron canadensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
Erysimum odoratum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	2	—	—	—	—
Euphorbia amygdaloides	—	—	—	—	—	—	—	—	—	—	—	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	—	—	—	—	—	—	—	—	—	—	—	—	—
E. cyparissias	—	—	0.2	—	—	—	—	0.2	—	—	—	—	0.2	—	0.2	—	—	—	2.5	—	0.2	—	0.2	0.2	2.5	—	—	—	—	—	—	—	—	2.5	—	—	—	—	0.2	0.2	—	0.2	—	—	5	0.2	0.2
E. polychroma	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Festuca gigantea	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
Festuca heterophylla	0.2	0.2	1.4	0.2	0.2	0.2	0.2	3	—	15	2.5	1.4	2.5	0.2	5	5	2.5	62.5	50	37.5	26	26	15	0.2	26	2.5	0.2	2.5	26	9	0.2	0.2	2.5	0.2	0.2	—	—	—	0.2	—	5	0.2	3	—	60	50	30
F. valesiaca-rupicola	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	0.2	15	0.2	—	—	—	—	—	—	—	—	0.2	2.5	15	37.5	—	—	—	—	—	—	15	—	—	0.2	—	—
Filipendula vulgaris	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	—	0.2	—	—	—	—	—
Fragaria elatior	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	—	—	—	—	—	—
F. vesca	1.4	0.2	1.4	0.2	0.2	20	5	3	—	0.2	—	—	0.2	0.2	8	—	0.2	2.5	—	—	—	—	0.2	0.2	—	0.2	5	—	0.2	—	—	—	0.2	—	—	3	5	8	—	10	10	0.2	5	25	—	0.2	—
Gagea lutea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—
Galeopsis pubescens	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
G. speciosa	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Galium aparine	—	—	—	0.2	0.2	—	—	—	—	0.2	—	9	0.2	0.2	—	—	0.2	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	9	—	—	—	—	—	—	—	—	—	—	—	—
G. mollugo	—	—	1.4	—	0.2	3	—	0.2	—	—	—	—	—	0.2	—	—	—	0.2	—	0.2	—	—	2.5	—	0.2	—	—	0.2	0.2	1.4	0.2	0.2	0.2	0.2	0.2	—	—	—	2	2	0.2	5	—	—	3	3	2
G. schultesii	15	9	15	1.4	9	2	5	3	4	0.2	50	0.2	0.2	0.2	25	30	15	1.4	2.5	2.5	0.2	—	2.5	15	—	2.5	8	2.5	2.5	0.2	0.2	0.2	2.5	0.2	0.2	0.2	3	4	—	3	10	—	7	0.5	—	—	—
G. verum	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	0.2	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Genista elatior	0.2	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	0.2	—	0.2	0.2	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	2	—	—	4	0.2	—	0.2	5	0.2
G. pilosa	37.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.4	—	—	—	—	—	—	—	0.2	—	2.5	15	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—
Geranium robertianum	—	—	—	—	—	3	—	—	0.2	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	3	0.2	—	—	0.2	—	—	—
G. sanguineum	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Table 2 (cont. — 4)

	A									B							C					D						E					F			AA			BB						CC		
Name of the facies	*Melica* facies									*Poa* facies							*Festuca heterophilla* facies					*Brachypodium* facies						*Luzula* facies					*Festuca rupicola* facies			Degraded *Melica* facies			Degraded *Poa* facies						Degraded *Festuca heterophylla* facies		
Numbering of sample quadrats	1	2	3	4	5	34	39	42	47	6	7	8	9	10	35	41	11	12	13	14	15	16	17	18	19	20	40	21	22	23	24	25	26	27	28	36	37	38	30	33	43	44	45	46	29	31	32
Geum urbanum	—	0.2	0.2	0.2	—	3	3	0.2	0.2	0.2	0.2	0.2	—	—	3	0.2	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	2	—	0.2	0.2	5	0.2	0.2	—	0.2	—	—	—
Glechoma hirsuta	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hedera helix	—	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Helleborus purpurascens	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Heracleum sphondylium	0.2	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—
Hieracium bauhinii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	0.2	—	—	0.2	—	—	—	—	2.5	1.4	0.2	—	—	0.2	—	—	—	—	2	—	—	0.2	—	—	0.2	—	—
H. maculatum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—
H. pilosella	—	—	—	—	—	—	—	—	—	15	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H. racemosum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	1.4	—	—	—	—	—	—	0.2	—	—	—	—	0.2	—	—	—	0.2	—	0.2	0.2	—	—	0.2	0.2	0.2	—	—	—
H. sabaudum	1.4	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	0.2	—	0.2	0.2	—	0.2	—	0.2	0.2	—	—	—	0.2	0.2	0.2	—	—	—	0.2	0.2	0.2	—	—	—	0.2	5	0.2
H. silvaticum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	0.2	—	—	—	0.2	—	—	—	—	0.2	—	0.2	0.2	0.2	0.2	0.2	—	—	—	—	0.2	—	—	0.2	—	0.2	—	—	—	—	—	0.2
H. umbellatum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—
Hypericum hirsutum	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	—	5	—	—	0.2	—	—	—
H. montanum	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H. perforatum	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	0.2	0.2	0.2	0.2	0.2	0.2	0.2	—	0.2	0.2	0.2	—	—	—	—	—	—	—	—	—	2	0.2	0.2	0.2	0.2	0.2	—	—
Hypochoeris maculata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Inula ensifolia	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
I. hirta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	2.5	—	0.2	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
I. salicina	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Iris graminea ssp. *pseudocyperus*	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—
I. variegata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lamium purpureum	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—
Lapsana communis	—	—	—	—	—	2	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	0.2	—	—	—	—	—	—
Laser trilobum	—	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Laserpitium latifolium	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lathyrus latifolius	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—
L. niger	—	0.2	—	—	0.2	—	0.2	—	—	—	—	—	—	0.2	0.2	0.2	—	2.5	0.2	0.2	0.2	—	0.2	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—
L. nissolia	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—
L. pratensis	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
L. vernus	0.2	0.2	0.2	0.2	0.2	—	0.2	—	—	—	—	—	—	1.4	—	0.2	—	—	—	1.4	—	0.2	—	0.2	—	0.2	—	1.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lilium martagon	—	—	0.2	0.2	—	—	0.2	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	0.2	—	0.2	—	0.2	0.2	—	—	—	—	0.2	—	—	—	0.2	—	—	0.2	—	—	—	—	—	—	—
Linaria genistifolia	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—
L. vulgaris	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lithospermum purpureo-coeruleum	—	0.2	—	—	—	—	—	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
Lotus corniculatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—
Luzula albida	2.5	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	2.5	0.2	—	—	1.4	—	0.2	—	15	26	2.5	0.2	1.4	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—
L. campestris	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	0.2	—	—	—	9	0.2	—	—	2.5	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—
Lychnis coronaria	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	3	—	—	3	0.2	0.2
L. flos-cuculi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
Lysimachia nummularia	—	—	0.2	—	—	0.2	—	0.2	—	—	—	—	—	—	—	0.2	—	15	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	0.2	—	—	—	—	—	—	—	—	—
Matricaria maritima ssp. *inodora*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
Melampyrum nemorosum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	0.2	—	—	—	—	—	0.2	—	0.2	—	0.2	0.2	1.4	—	—	—	50	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—
Melica nutans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
M. uniflora	2.5	87.5	37.5	75	2.5	40	60	70	45	2.5	1.4	2.5	0.2	—	0.2	0.2	1.4	—	0.2	0.2	0.2	1.4	0.2	0.2	—	—	0.2	—	—	0.2	—	—	—	—	—	4	0.2	20	—	15	5	—	—	—	—	—	—
Melittis grandiflora	—	0.2	0.2	—	0.2	—	—	—	—	—	—	0.2	0.2	—	2	0.2	0.2	0.2	—	—	0.2	—	0.2	1.4	0.2	0.2	0.2	0.2	—	—	—	0.2	0.2	—	—	—	4	0.2	—	0.2	0.2	—	5	—	—	—	—
Moehringia trinervia	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Molinia arundinacea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—
Mycelis muralis	—	—	—	—	—	—	0.2	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	0.2	—	—	—	—	—

Table 2 (cont. — 5)

Name of the facies	*Melica* facies									*Poa* facies							*Festuca heterophylla* facies					*Brachypodium* facies						*Luzula* facies					*Festuca rupicola* facies			Degraded *Melica* facies			Degraded *Poa* facies						Degraded *Festuca heterophylla* facies		
	A									B							C					D						E					F			AA			BB						CC		
Numbering of sample quadrats	1	2	3	4	5	34	39	42	47	6	7	8	9	10	35	41	11	12	13	14	15	16	17	18	19	20	40	21	22	23	24	25	26	27	28	36	37	38	30	33	43	44	45	46	29	31	32
Myosotis arvensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
M. hispida	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Neottia nidus-avis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—
Orchis militaris	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—
Origanum vulgare	—	—	—	—	—	—	—	0.2	—	—	0.2	—	—	—	0.2	—	—	—	2.5	0.2	0.2	0.2	0.2	0.2	2.5	—	—	—	—	0.2	—	—	0.2	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—
Orobanche vulgaris	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—
Parietaria officinalis	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Peucedanum alsaticum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—
P. cervaria	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phleum phleoides	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.4	0.2	0.2	0.2	0.2	—	15	—	—	—	0.2	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pimpinella saxifraga	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—
Plantago media	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—
Platanthera bifolia	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Poa angustifolia	—	—	0.2	—	—	—	—	—	—	—	—	—	—	9	—	—	1.4	0.2	0.2	—	2.5	—	9	—	37.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—	—	—
P. nemoralis	0.2	—	1.4	—	0.2	5	5	5	15	37.5	37.5	50	75	2.5	35	40	0.2	0.2	2.5	2.5	0.2	9	26	2.5	9	2.5	40	2.5	2.5	—	0.2	9	—	1.4	—	—	0.2	—	60	30	30	30	40	20	10	—	30
P. trivialis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—
Polygonatum multiflorum	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
P. odoratum	—	—	2.5	—	0.2	—	0.2	0.2	—	—	—	—	0.2	—	—	—	—	0.2	—	—	—	0.2	0.2	0.2	0.2	0.2	0.2	—	—	0.2	—	0.2	0.2	—	—	—	0.2	—	—	—	—	—	—	—	0.2	—	0.2
Polygonum aviculare	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
P. dumetorum	—	—	—	—	—	2	0.2	0.2	15	—	—	1.4	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.5	—	—	—	0.2	—	2	0.2	—	—	—	—	—	—
P. minus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
Polypodium vulgare	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Potentilla alba	—	—	2.5	—	—	3	0.2	—	—	—	—	—	—	—	2	0.2	—	15	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—	0.2	0.2	—	—	0.2	0.2	—	—	—	0.2	—	—
P. argentea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
P. heptaphylla	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P. micrantha	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—
Primula veris	—	—	0.2	—	0.2	0.2	0.2	0.2	—	0.2	2.5	—	—	0.2	2	—	0.2	0.2	0.2	0.2	—	—	0.2	—	0.2	0.2	0.2	—	0.2	1.4	0.2	—	0.2	—	50	0.2	—	—	—	0.2	0.2	—	—	0.2	—	—	—
Prunella vulgaris	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	0.2	—	—
Pteridium aquilinum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—
Pulmonaria mollissima	—	—	2.5	—	0.2	0.2	0.2	2	—	1.4	0.2	—	—	0.2	4	—	—	0.2	—	0.2	0.2	0.2	0.2	—	0.2	0.2	0.2	0.2	—	—	—	—	2.5	—	—	0.2	—	0.2	—	0.2	—	—	—	—	—	—	—
P. officinalis	0.2	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—
Ranunculus auricomus	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	0.2	—	—	0.2	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—
R. ficaria	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—
R. polyanthemos	—	—	0.2	—	—	—	0.2	—	—	0.2	—	—	—	—	0.2	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	0.2	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—
R. repens	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
Rosa gallica	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—
Rubus fruticosus s. l.	0.2	—	—	0.2	0.2	3	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	10	10	—	—	—	—	0.2	0.2	—	—	—
R. idaeus	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rumex sanguineus	—	—	0.2	—	—	2	0.2	—	—	—	—	—	—	—	—	—	—	2.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	3	5	—	—	—	—	—	—
Salix caprea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
Salvia glutinosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—
S. nemorosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—
Sanicula europaea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—
Scrophularia nodosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sedum acre	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
S. maximum	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	—
S. sexangulare	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	0.2	—	—	—	—	—	—	—	2.5	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Senecio vulgaris	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—

Table 2 (cont. — 6)

	A									B						
Name of the facies	*Melica* facies									*Poa* facies						
Numbering of sample quadrats	1	2	3	4	5	34	39	42	47	6	7	8	9	10	35	41
Serratula tinctoria	0.2	—	0.2	0.2	0.2	0.2	—	0.2	—	—	—	—	—	—	—	2
Silene cucubalus	—	—	0.2	—	—	—	0.2	0.2	—	0.2	—	—	—	—	—	—
S. nutans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
S. viridiflora	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—
Solidago virga-aurea	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—
Stachys recta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Stellaria holostea	9	9	15	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	—	15	0.2	—	0.2
S. media	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Symphytum nodosum	—	—	—	0.2	0.2	3	0.2	—	—	—	—	0.2	—	0.2	5	—
Taraxacum officinale	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—
Teucrium chamaedrys	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Torilis japonica	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	0.2
Trifolium alpestre	0.2	—	0.2	—	0.2	0.2	—	—	—	0.2	—	—	—	0.2	2	—
T. aureum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T. campestre	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T. medium	0.2	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—
T. montanum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T. ochroleucum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T. rubens	0.2	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
Urtica dioica	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—
Valeriana officinalis	—	—	0.2	0.2	—	0.2	—	0.2	—	0.2	—	—	—	0.2	0.2	—
Veratrum nigrum	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
Verbascum austriacum	—	—	0.2	—	—	—	—	—	—	—	0.2	—	—	—	—	—
V. phoeniceum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Veronica chamaedrys	2.5	0.2	2.5	0.2	0.2	0.2	—	0.2	0.2	9	0.2	0.2	1.4	0.2	—	0.2
V. dentata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
V. hederifolia	—	—	—	—	—	—	—	—	—	0.2	—	—	0.2	—	—	—
V. officinalis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
V. spicata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
V. teucrium	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—
Vicia cassubica	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2
V. dumetorum	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—
V. pisiformis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
V. sepium	—	—	—	0.2	—	0.2	—	—	—	—	—	0.2	—	—	—	—
V. sparsiflora	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
V. tenuifolia	—	—	—	—	0.2	—	—	—	—	—	—	—	0.2	0.2	—	—
V. tetrasperma et hirsuta	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—
Viola alba	—	0.2	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
V. arvensis	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
V. cyanea	0.2	2.5	0.2	0.2	—	—	—	—	—	0.2	2.5	—	9	—	0.2	—
V. hirta	—	—	—	—	0.2	—	—	0.2	—	—	—	0.2	—	—	—	—
V. mirabilis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
V. odorata	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—
V. riviniana	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
V. silvestris	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—
Viscaria vulgaris	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—

	C					D						E					F			AA			BB						CC		
Name of the facies	*Festuca heterophylla* facies					*Brachypodium* facies						*Luzula* facies					*Festuca rupicola* facies			Degraded *Melica* facies			Degraded *Poa* facies						Degraded *Festuca heterophylla* facies		
Numbering of sample quadrats	11	12	13	14	15	16	17	18	19	20	40	21	22	23	24	25	26	27	28	36	37	38	30	33	43	44	45	46	29	31	32
Serratula tinctoria	0.2	0.2	—	—	—	0.2	0.2	—	—	—	0.2	0.2	0.2	—	—	0.2	0.2	—	—	0.2	—	—	—	2	—	—	0.2	—	—	—	—
Silene cucubalus	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—
S. nutans	—	—	0.2	0.2	—	0.2	—	0.2	—	—	—	2.5	0.2	1.4	9	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—
S. viridiflora	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	0.2	—	—	0.2	—	0.2
Solidago virga-aurea	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	0.2	—	—	—	—	0.2	3	0.2	—	—	—	—	—	—	—	—	—
Stachys recta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—
Stellaria holostea	9	—	0.2	0.2	0.2	0.2	—	9	2.5	2.5	—	—	—	—	—	0.2	9	—	—	3	0.2	—	—	—	—	—	—	—	—	—	—
S. media	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—	—	—
Symphytum nodosum	0.2	0.2	—	—	—	—	—	—	—	0.2	—	—	0.2	—	—	—	0.2	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—
Taraxacum officinale	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Teucrium chamaedrys	—	—	2.5	0.2	0.2	0.2	2.5	0.2	15	—	—	—	—	0.2	—	—	—	9	0.2	—	—	—	0.2	—	0.2	0.2	—	—	0.2	0.2	0.2
Torilis japonica	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
Trifolium alpestre	0.1	1.4	1.4	0.2	0.2	0.2	0.2	0.2	9	—	—	0.2	2.5	—	0.2	0.2	0.2	0.2	0.2	—	—	—	0.2	—	0.2	—	—	—	3	0.2	0.2
T. aureum	—	—	0.2	—	—	—	0.2	0.2	—	—	—	0.2	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T. campestre	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T. medium	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T. montanum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—
T. ochroleucum	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T. rubens	—	—	0.2	—	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Urtica dioica	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	0.2	—	—	—
Valeriana officinalis	—	0.2	—	0.2	—	1.4	0.2	—	0.2	0.2	0.2	0.2	0.2	—	—	—	0.2	0.2	0.2	—	—	0.2	—	—	0.2	—	0.2	—	—	—	—
Veratrum nigrum	0.2	2.5	—	—	—	—	1.4	0.2	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Verbascum austriacum	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	1.4	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	—
V. phoeniceum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—
Veronica chamaedrys	0.2	2.5	0.2	2.5	0.2	0.2	0.2	2.5	0.2	0.2	—	0.2	0.2	1.4	1.4	0.2	0.2	0.2	—	—	—	—	0.2	0.2	0.2	3	0.2	—	0.2	0.2	—
V. dentata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—
V. hederifolia	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
V. officinalis	0.2	—	—	—	0.2	—	1.4	—	—	—	—	0.2	2.5	0.2	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	—	0.2	0.2	0.2
V. spicata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—
V. teucrium	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Vicia cassubica	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
V. dumetorum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
V. pisiformis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2
V. sepium	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	0.2	—	0.2	—	—	—	—	—	—	—
V. sparsiflora	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	0.2	—	—
V. tenuifolia	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—
V. tetrasperma et hirsuta	0.2	—	—	—	0.2	—	—	—	—	—	—	—	0.2	—	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—
Viola alba	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
V. arvensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—
V. cyanea	0.2	—	0.2	0.2	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—	—	0.2	0.2	—	0.2	—	—	—	0.2	—
V. hirta	—	0.2	—	—	0.2	—	2.5	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—
V. mirabilis	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
V. odorata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—
V. riviniana	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	0.2	—	—	—	—	—	—
V. silvestris	0.2	0.2	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	0.2	—	—	0.2	4	—	—	—	—	—	—	—	—	—
Viscaria vulgaris	0.2	0.2	9	0.2	0.2	0.2	0.2	0.2	0.2	—	—	0.2	0.2	0.2	0.2	0.2	—	—	0.2	—	—	—	0.2	—	—	0.2	—	—	—	—	—

Fig. 1. The position of stands of *Quercetum petraeae-cerris* facies on the W—R continuum. [The basis of representation of stands on the W—R continuum is the calculation of averages of W- and R-values (ZÓLYOMI 1964) of all species in the stands. Note that high W-values refer to favourable water supply, decrease of R-value shows the increasing acidity of soil]

It is noted that the way and origin of perturbation may be different. Here and there regular trampling by tourists influences the vegetation, in other places the increasing game stock is responsible for the disturbance. Cars and tractors repeatedly crossed several stands, thus facilitating the spread of new species along the tracks and, simultaneously, annihilating some indigenous species. Unfortunately, we have insufficient information for the comparison of perturbation effects, as the duration and intensity of the disturbance are unknown.

The effects of perturbation strike the eye many times. Considering only our own relevés, the possible effects may be summarized as follows:*

1. The increase in the frequency of nitrophilous forest species, such as *Urtica dioica*, *Alliaria petiolata*, *Torilis japonica*, *Galeopsis speciosa*, etc.

2. The infiltration of some species, such as *Epilobium roseum*, *E. parviflorum*, *E. tetragonum*, *Festuca gigantea* and *Melica nutans* from the neighbouring mesophilous forests.

3. The occurrence of meadow species, such as *Alopecurus pratensis*, *Poa trivialis*, *Lychnis flos-cuculi*, *Briza media*, *Deschampsia caespitosa*, *Ranunculus repens*, and *Cardamine pratensis*, etc.

* At this phase of the study, any statement on how the adventive-accident species are associated with a given facies would be unsubstantiated.

4. The appearance of ruderal and ubiquitous species, such as *Cirsium lanceolatum*, *Polygonum aviculare*, *Matricaria inodora*, *Agropyron repens*, *Erigeron canadense*, *Senecio vulgaris*, *Plantago media*, and *Taraxacum officinale*, etc.

What is undetectable or hardly observable in the field is the simultaneous effect of the above factors on the indigenous flora. Clearly, this effect manifests itself through the change of species abundance and the disappearance of some species.

HORÁNSZKY (1964) published his relevés from the turkey oak—sessile oak woods of the Szentendre-Visegrád Mts. in tabular form. For the present study five relevés for each facies were selected from that table, so that variability within the facies was as high as possible in the sample. The total number of relevés is 25. In addition, relevés were taken in 1982–1983 in the perturbed stands and in the neighbouring, relatively intact woods. The sampled area was 20×20 m for each relevé; the percentage cover of species was estimated.

The considerations given in the Introduction and our impressions regarding the different perturbation status of facies led to the following questions. We would like to investigate

1. whether the coenological separation and co-ordination of the facies is similar or dissimilar,

2. what the response of entities to perturbation is and how stable their composition is, and

3. whether there is any relationship between 1 and 2 ?

Methods

The total number of species in the facies and perturbed derivatives, and the average number of species and its standard deviation for the relevés were determined in order to compare the species richness of facies and to evaluate changes owing to perturbation.

Multivariate analyses (cluster analysis and ordination) were used to reveal the resemblance structure of facies and derivatives. Our aim was to see whether an a priori classification of facies based on the dominant species is congruent with objective classifications using all the species. Also, question 1 raised at the end of the previous section may be rephrased: How sharp is interfacies segregation and how high is the intrafacies compositional similarity ? What is the influence of dominant species upon the species composition and abundance ? Is the quantitative distribution of species merely affected by the abundant species or rather, are the qualitative aspects more important ?

These problems will be investigated by the application of two types of resemblance coefficients, one based on cover estimates and the other using presence/absence data.

Data analyzed by multivariate methods

The raw data matrix contains cover estimates for 288 species in 47 relevés. The data were neither standardized nor transformed during the analysis in order to keep the quantitative differences, which may prove significant in the distinction of facies differing in the frequency distribution of species.

The fact that very few dominants occur in any facies and much more rare species are present was also considered. The distribution of species has a striking peak, so that parametric statistics seem inappropriate even after data transformation (LEGENDRE, L. and LEGENDRE, P. 1983).

An additional problem is whether the double zeros should be considered in the comparison of relevés (LEGENDRE, L. and LEGENDRE, P. 1983). We know that the species composition of rich stands of the facies studied originates from a rich flora (see Table 3). Thus, the probability that the same species occur in all stands of a facies is very low. The absence of rare species from both relevés being compared is a probabilistic event, rather than the indication of unfavourable environmental conditions. Stands poor in species are also common, these contain only a small subset of the species (e.g. in perturbed derivatives and in the *Luzula* facies), and these subsets may differ with relevés. If the double zeros were considered in the comparisons, very high similarity would result, for example, for two species poor relevés that have very few species in common. Such a comparison is obviously inadequate in the present case, as double absence has no ecological implications. Thus, the relevés were compared with asymmetric coefficients (in the sense of LEGENDRE, L. and LEGENDRE, P. 1983), which disregard the double zeros.

The relevés were classified by divisive information analysis (LANCE and WILLIAMS 1968, PODANI 1979), which uses presence/absence data. Agglomerative clustering methods based on either presence/absence or cover were also used. The ordination method selected for the present study is principal co-ordinates analysis, which accepts any kind of resemblance matrices as input.

Multivariate analyses

Two variants of divisive "association-analysis" were used: 1. divisive information analysis (LANCE and WILLIAMS 1968) in which the criterion for division is the reduction of "information content" or "information fall"; and 2. PODANI's (1979) information analysis, which uses a maximum likelihood criterion as the divisive parameter.

Since the probability of misclassification is much lower for the agglomerative clustering methods, especially in our case when there is a data set expressing cover relations, some agglomerative clustering methods were also applied.

All these agglomerative methods are polythetic and r-hierarchical (route-optimizing). These are: furthest neighbour sorting (complete linkage) and sum of squares agglomeration (WARD's method).

The resemblance matrices were calculated according to the following coefficients:

Presence/absence data	Cover data
Sørensen index	Czekanowski's percentage similarity
Chord distance	Chord distance

These coefficients are not sensitive to double zeros. CHORD distance, contrary to the EUCLIDEAN distance, is not influenced by the actual ranges of cover values. Thus, its use avoids the paradox situation in which two relevés, having no species in common, are more similar than two which share most species but with excessive differences in cover values.

The clustering methods are known to be responsible for overemphasizing discontinuities among the objects. They may force a separation into "discrete" classes even if the vegetation

analyzed is continuous in nature. Owing to this disadvantage, it is advisable to complement classification studies with ordinations. Ordinations are useful because they treat the total variability in a resemblance matrix and detect the most important underlying relationships and main trends in the data.

As mentioned above, we used principal co-ordinates analysis (PCoA) for scaling. The application of this procedure is not restricted to quantitative descriptors, as the nature of the resemblance coefficient will determine the data types allowed. Then, it is possible to construct ordinations so that the distortion caused by double zeros is avoided. In the present study principal co-ordinates ordinations were based on the same resemblance coefficients that were used for agglomerative clustering (SORENSEN index, chord distance and CZEKANOWSKI index).

Computer programs ASSINF, NCLAS and PRINCOOR from the SYN-TAX II package (PODANI 1980, 1984) were used to calculate cluster analyses and ordinations.

Results

Total and average number of species in the facies

Table 2 shows the percentage cover values of species in the relevés. The number of species in each facies, the average species number of relevés, the standard deviation of this average and the coefficient of variation (CV) are given in Table 3. The changes in species number upon the influence of perturbations are summarized in Table 4.

The flora is the richest in the *Melica* facies; the other two zonal facies (*Festuca heterophylla* and *Poa nemoralis*), and the *Brachypodium* facies have also a high species number. Accordingly, the number of potential species combinations is also the highest in these facies. The lowest species number

Table 3

Total and average species numbers in facies

Facies	Total species number	Average species number and standard deviation	CV%
Melica uniflora	141	47 ± 3.67	23.6
Poa nemoralis	121	39 ± 2.08	14.2
Festuca heterophylla	128	51 ± 4.85	21.3
Brachypodium pinnatum	130	52 ± 3.78	17.9
Luzula nemorosa	106	45 ± 3.30	16.3
Festuca rupicola	89	44 ± 5.56	21.9
Perturbed *Melica uniflora*	68	41 ± 2.51	10.6
Perturbed *Poa nemoralis*	149	51 ± 5.48	26.4
Perturbed *Festuca heterophylla*	67	39 ± 5.25	19.1

Table 4

Percentage changes and their direction for the average (a) and total (b) species number

Facies	Species number in original stands		Species number in perturbed stands	Percentage change
Festuca heterophylla	*a* 51	>	39	24
	b 128	>	67	48
Poa nemoralis	*a* 39	<	51	30
	b 121	<	149	20
Melica uniflora	*a* 47	>	41	13
	b 141	>	68	53

was indicated in the degraded versions of the *Melica* and *Festuca heterophylla* facies, in the *Festuca rupicola* facies. The *Luzula* facies may also be considered as being species poor. Trends in the change of average species number are similar to the change of the total number of species. Note that in species rich facies the average species number of stands is only about one-third of the total for that facies. In the species poor types this decrease is less than 50%. These changes may also indicate the compositional variability of the original, undisturbed facies.

Association analysis

The classification of all relevés by the divisive information analyses is shown in Fig. 2 only in the case of PODANI's version (1979), because the two algorithms produced similar results.

The first division is due to *Teucrium chamaedrys*, and provides two big clusters. In the first in which this species is present has the three relevés of the *Festuca heterophylla* facies, all the three relevés from its degraded versions, the relevés of the *Festuca rupicola* facies and 70% of the relevés from the *Brachypodium* facies. [*Teucrium chamaedrys*, as a "*Quercetea pubescenti-petraeae*" element characterizes the *Festuca heterophylla* and *Brachypodium* facies with its constancy (frequency) value II and IV, respectively, cf. HORÁNSZKY 1964].

The other big group from which *Teucrium chamaedrys* is absent comprises the *Melica* and *Poa* facies, their degraded variants and the *Luzula* facies. This group is subdivided according to *Luzula luzuloides* and *Calamagrostis arundinacea* (both are acidifrequent *Quercetea robori-petraeae* species); the *Luzula* facies and the degraded *Melica* facies are separated from the others. The ecological interpretation of the other subdivisions seems doubtful, it is

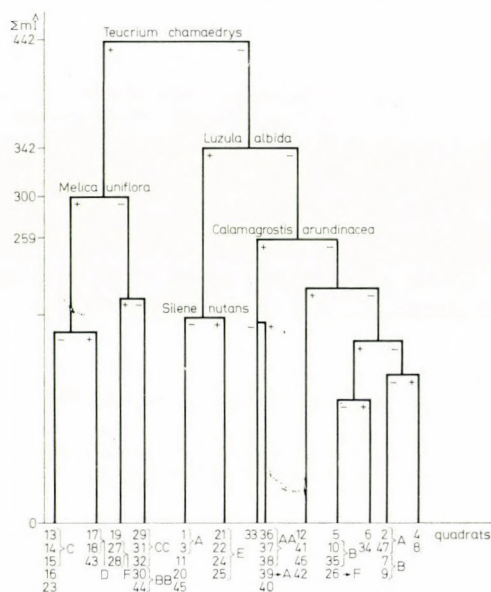



Fig. 2. Hierarchy for quadrats (see Table 2) obtained with PODANI's (1979) version of association analysis. (A = *Melica* facies; B = *Poa* facies; C = *Festuca heterophylla* facies; D = *Brachypodium* facies; E = *Luzula* facies; F = *Festuca rupicola* facies; AA = degraded *Melica* facies; BB = degraded *Poa* facies; CC = degraded *Festuca heterophylla* facies)

likely that species absent from some quadrats by chance are selected as divisive ones.

This classification suggests that, based on the presence/absence of species, the poor *Luzula* facies and the degraded versions of the *Melica* and *Festuca heterophylla* facies form homogeneous, separated groups.

Agglomerative clustering

The general structure of dendrograms obtained by different presence/absence coefficients is fairly similar (Figs 3, 4). The objects are fused only in pairs at relatively high levels, whereas at lower levels the relevés from different facies are mixed. However, the separation of degraded *Festuca heterophylla* and *Melica* types is striking in the classifications that use Sørensen index and chord distance. Furthermore, the *Luzula* facies is also pretty well isolated. The least homogeneous is the *Festuca heterophylla* facies; and the *Melica* and *Poa* facies are also fragmented into smaller groups. The originally heterogeneous composition is uniformized by perturbation, and the derived versions (especially in case of the *Festuca heterophylla* and *Melica* facies) exhibit high intrafacies similarity. It is established that the degraded stands of the *Festuca heterophylla* facies are taken far apart from the starting situation in the pres-

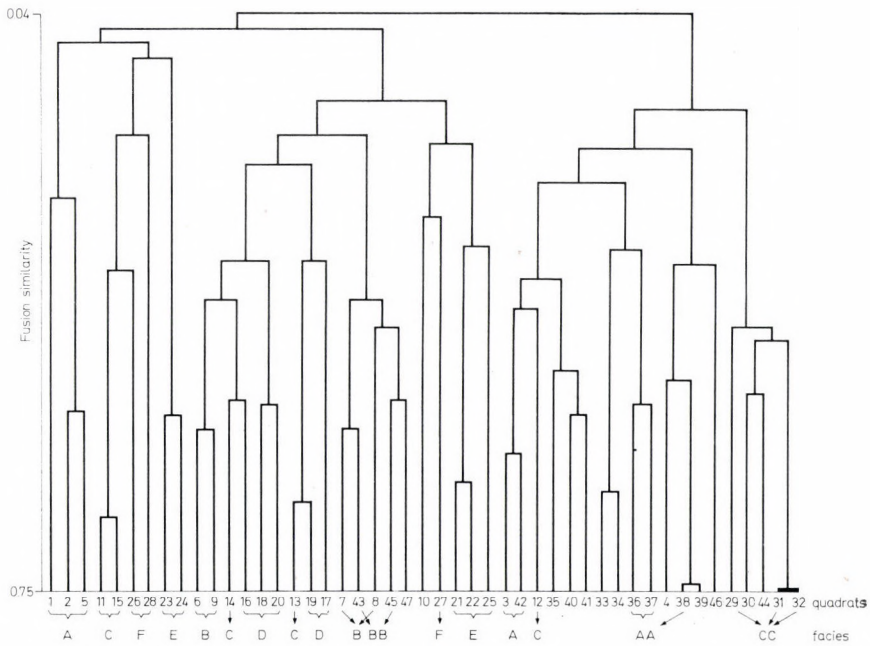
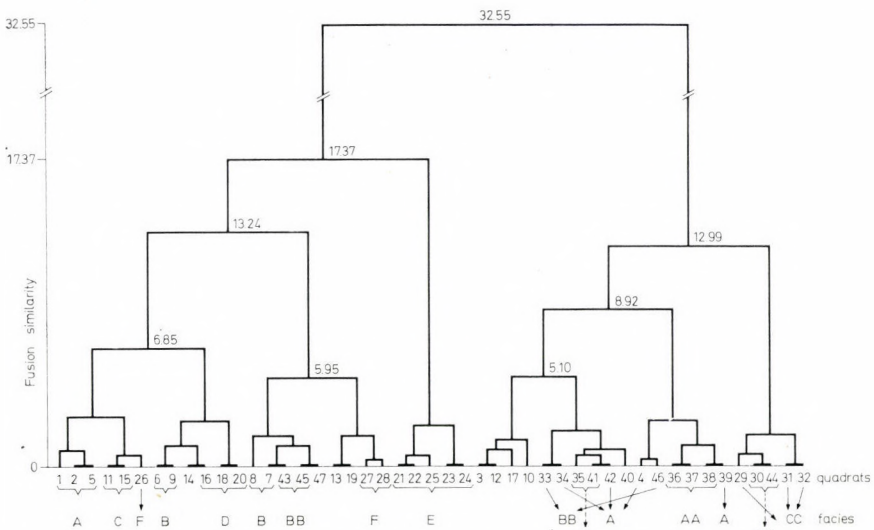
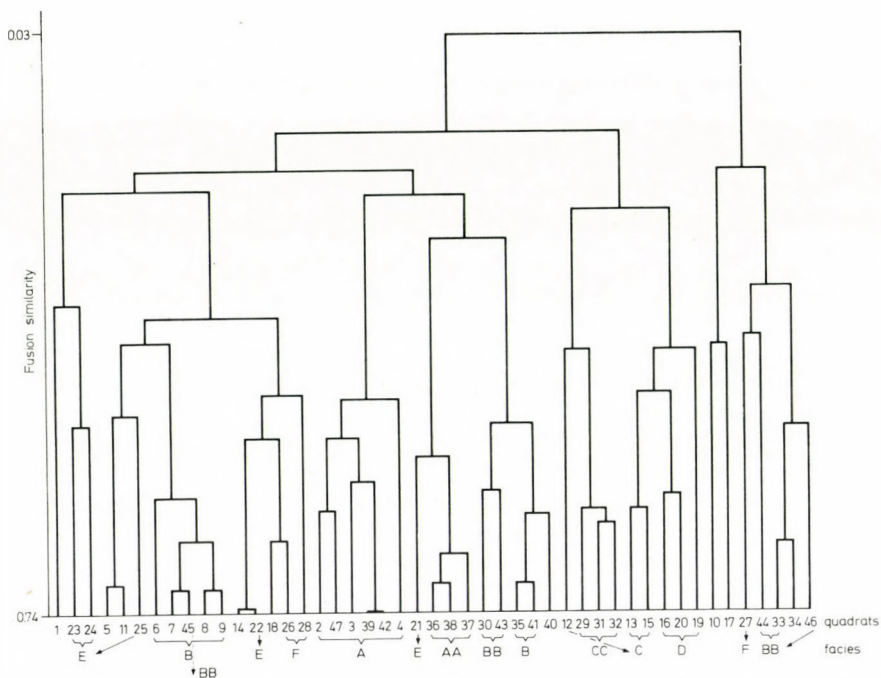



Fig. 7. Ordination of sampling plots with the first 3 principal coordinate axes (PCoA was based on the CZEKANOWSKI's resemblance matrix). *(a)* Representation of quadrats on the 1st and the 2nd principal coordinate axes.

ence/absence case, whereas most degraded *Melica* and *Poa* stands are joined with the undisturbed stands at low levels. The separation of the *Festuca rupicola* and *Brachypodium* facies is relative and uncertain.

The similarity structure of stands is quite different in the quantitative case (Figs 5, 6).

The clustering results based on binary and quantitative data are similar in that (1) the stands of the degraded *Festuca heterophylla* and the degraded *Melica* facies have high intrafacies similarity, and (2) compared with all the other facies, the *Festuca heterophylla* and *F. rupicola* facies are strongly fragmented, they apparently do not form distinct clusters (intrafacies segregation). The differences are as follows: (1) the stands of the *Luzula* facies are less homogeneous in the quantitative case than when presence/absence data are considered. (2) Contrary to the binary case, based on cover values well-separated clusters are formed by the quadrats from the *Poa* and *Melica* facies.

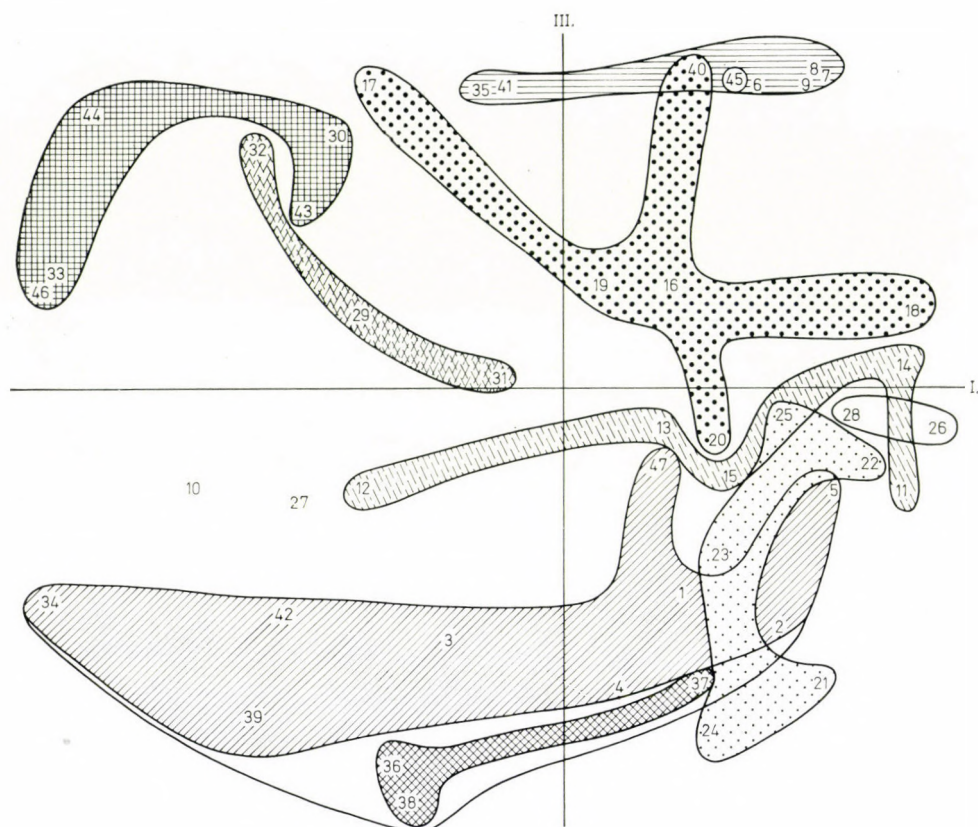



Fig. 7. (b) Representation of quadrats on the 1st and the 3rd principal coordinata axes

It shows that the denominating dominant species are decisive in determining the high intrafacies similarity as well as interfacies segregation. On the other hand, the dominance of one or two species does not influence the quantitative picture.

Principal co-ordinates analysis

The ordination of the presence/absence data agrees well with the classifications; separate homogeneous groups are formed by the degraded *Festuca heterophylla* and the *Luzula* facies. It is striking that the *Luzula* facies is more isolated in the PCoA ordinations.

In the ordination of cover data compared by the CZEKANOWSKI index and chord distance, all facies are relatively well separated (Figs 7, 8). A band-like arrangement is found along axis 2, which is thus interpretable as a dimension corresponding to zonality and habitat conditions (Figs 7a, 8a).

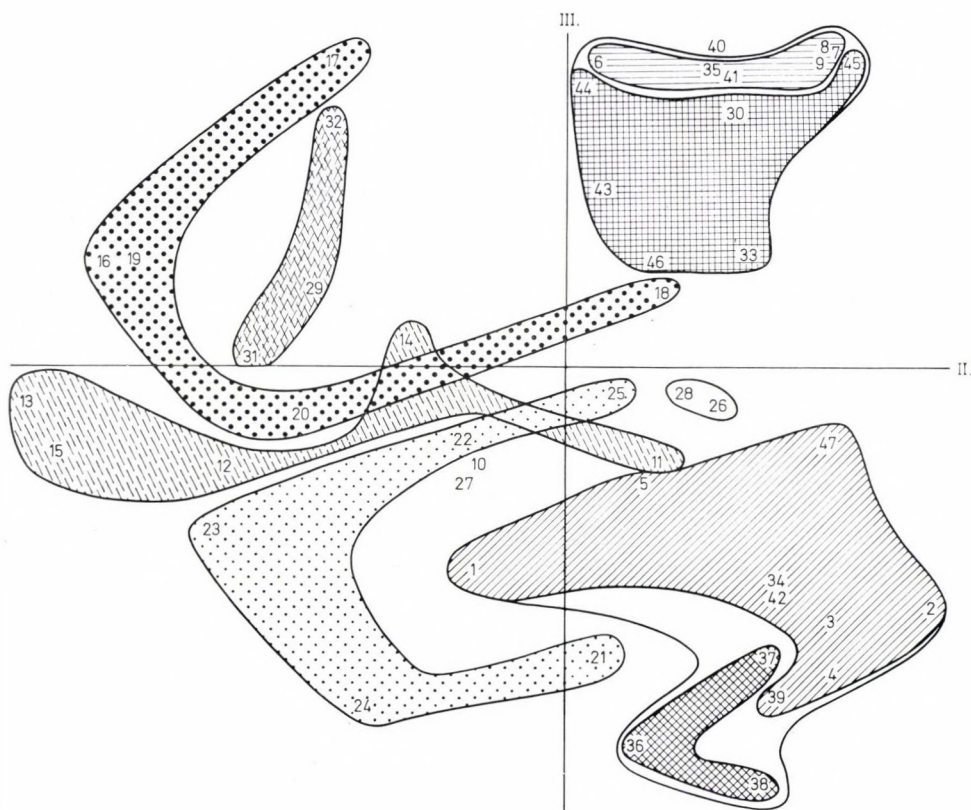



Fig. 7. (*c*) Representation of quadrats on the 2nd and the 3rd principal coordinate axes

In the plane of dimensions 1–2 and 2–3 (Figs 7a, 7c, 8a, 8c), the band-like arrangement of the *Melica, Poa, Brachypodium* and the *Festuca heterophylla* facies, in that order, is obvious. All degraded versions are close to their corresponding original facies. The degraded *Melica* and the degraded *Festuca heterophylla* stands are also relatively close to the natural facies, but are segregated, homogeneous groups. The degraded stands of the *Poa* facies are less distinct from the undisturbed stands.

Discussion

The multivariate analyses of species composition offer a possibility to compare the facies and their derivatives. Intrafacies similarity refers to the inherent property co-ordination (Juhász-Nagy and Vida 1978), whereas the interfacies segregation is an external property (identifiability). Clearly, these

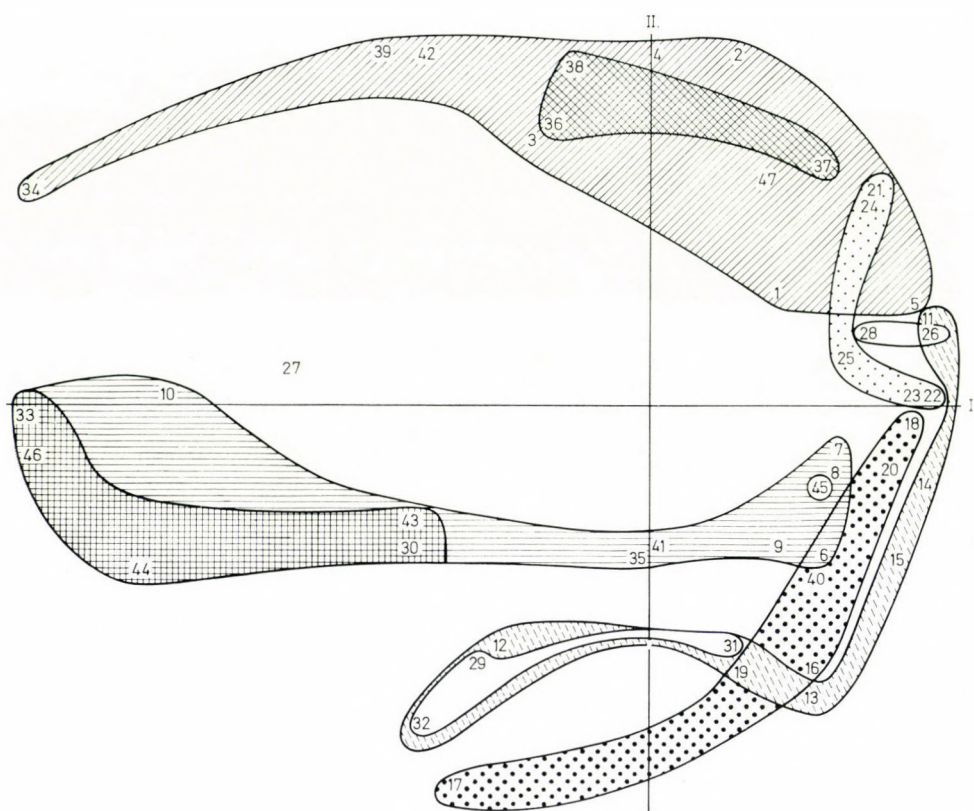



Fig. 8. Ordination of sampling plots with the first 3 principal coordinate axes (PCoA was based on the resemblance matrix constructed by chord distances from cover data). *(a)* Representation of quadrats on the 1st and the 2nd principal coordinate axes.

two properties are not necessarily associated with each other. Our study provides good examples: the *Calamagrostis* facies (= degraded *Melica* facies) has high intrafacies similarity but no segregation, whereas the *Festuca heterophylla* facies is well separated in several ordination dimensions but its homogeneity is low.

The results suggest that the facies of the turkey oak—sessile oak wood have unequal phytosociological rank, if segregation and homogeneity are considered. The common (quasi-zonal) and rare (edaphic) facies must be treated separately. There is little discontinuity among the common facies (*Melica, Poa, Festuca heterophylla*) on presence/absence basis, because species composition has great variability. The dominance of a single species is decisive especially in the *Melica* and *Poa* facies: considering cover values the facies form homogeneous groups and their separation is more explicit. The unam-

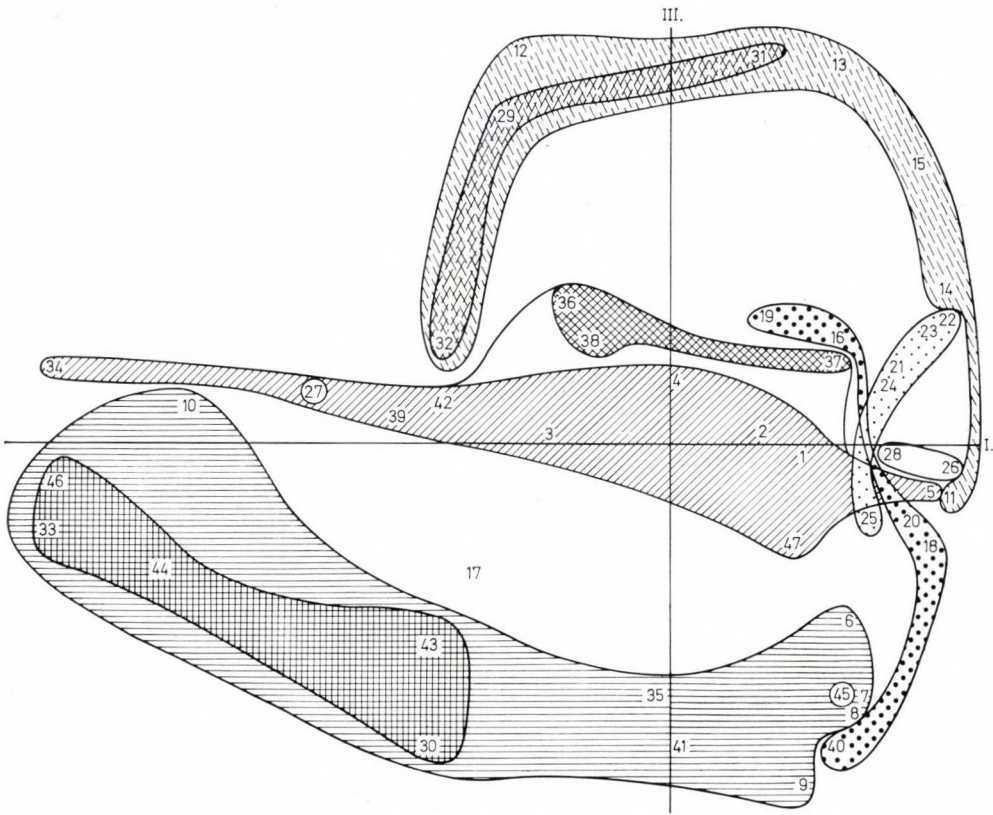



Fig. 8. (b) Representation of quadrats on the 1st and the 3rd principal coordinates axes

biguous topological separation of the common facies along an altitudinal and habitat gradient is an essential property.

Of the rare facies, the *Luzula* stands show high "inner" uniformity and rather good "outer" separation, as confirmed by all clustering and ordination methods (especially in the presence/absence case). A possible reason for this is that species number is relatively low owing to the extreme habitat; species requiring deeper forest soils are all absent, whereas the species with narrow tolerance appear in most stands.

The perturbed stands may be characterized as follows. Presumably, the process of degradation is different in each facies. The after-perturbation changes in the *Melica* and *Festuca heterophylla* facies are manifested in the decrease of species number which, in turn, leads to highly uniform stands. A possible way of deterioration in the *Melica* facies is that *Calamagrostis* becomes abundant, in such stands the degradation did not cause a significant departure from the original species composition. The degradation of the *Poa nemoralis* facies is

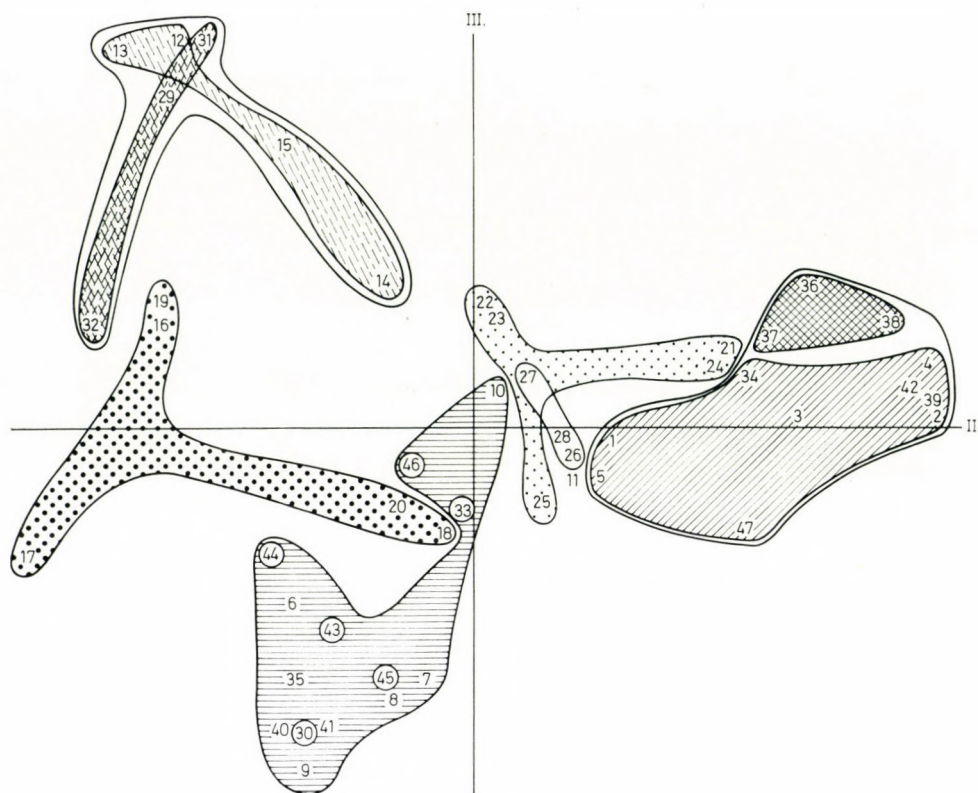



Fig. 8. (*c*) Representation of quadrats on the 2nd and the 3rd principal coordinata axes

associated with an increase of the total and average number of species. This increase, if we consider the above-mentioned decreases in species numbers, is striking: we do not know whether the *Poa* facies has been over a "passive" successional stage (the deterioration) and new species started to immigrate, or whether deterioration has not taken place at all. In any case, the heterogeneity of species composition is higher in the degraded stands than in the natural facies, which is not too uniform anyway.

Perturbed stands of the rare facies have not yet been found. We assume that the *Luzula* facies poor in species resulted from a slow and continuous deterioration in a habitat that was more unfavourable anyway. The poor elutriated soil probably selects among the immigrant species, and further response to perturbation is minimal. The final result is the retreat of flowering plants and the spread of certain moss species (BORHIDI, personal communication). This is the facies which exhibits a definite intrafacies similarity, as the expression of inner co-ordination, associated with a resistance to the penetra-

tion of alien species. In this regard the *Luzula* facies is an antagonist of the *Poa* facies.

The position and the level of degradation of the *Festuca rupicola* facies are doubtful. The three relevés provide insufficient information for drawing far reaching conclusions. It is likely that this represents another type of degradation. It is known (Horánszky 1964) that *Festuca rupicola* became dominant due to soil erosion and the abundance of this species influences the proportion of other species and regulates regeneration processes. Our studies appear to indicate the distinctness of this facies.

It is emphasized that the picture on the facies of the turkey oak– sessile oak woods outlined above concerns only the Szentendre-Visegrád Mountains, provided that the relevés are representative enough (there is much more to do in this regard in the future). It is expected that in other regions, under different zonality conditions, the co-ordination, segregation and relative position of facies will change, with the changing composition.

REFERENCES

Danszky, I., Rott, F. (eds): Magyarország erdőgazdasági tájainak erdőfelújítási, erdőtelepítési irányelvei és eljárásai. Általános irányelvek, erdő- és termőhelytípus térképezés (Guiding principles and procedures of forest regeneration, afforestation in Hungarian forestry regions. General principles, mapping of forest- and habitat-types). Budapest, 346. pp.

Horánszky, A. (1960): Über das Problem der Bewaldung im Andesitgebirge (Ein neuer Florendistrikt im Ungarischen Mittelgebirge). *Ann. Univ. Scient. Budapest, Sect. Biol.* **3:** 215–224.

Horánszky, A. (1964): *Die Wälder des Szentendre-Visegráder Gebirges.* (Die Vegetation Ungarischer Landschaften 4.) Budapest, 288. pp.

Jakucs, P. (1980): Rekonstruktion der potentiellen primären organischen Stoffmenge und ihrer Produktion in Ungarn. *Acta Bot. Acad. Sci. Hung.* **26:** 71–82.

Juhász-Nagy, P., Vida, G. (1978): Szupraindividuális organizáció (Supraindividual organization). In Csaba, Gy. (ed.): *Biológiai Szabályozás* (Biological Control). Budapest, 337–406.

Kovács, M. (1975): *Beziehung zwischen Vegetation und Boden. Die Bodenverhältnisse der Waldgesellschaften des Mátragebirges.* (Die Vegetation Ungarischer Landschaften 6.) Budapest, 363. pp.

Kovács, M., Podani, J. (1979): Zönologische Untersuchung der Traubeneichen-Zerreichenwälder der Tarna-Gegend (Nordungarisches Mittelgebirge). *Phytocoenologia* **6:** 439–454.

Lance, G. N., Williams, W. T. (1968): Note on a new information-statistics classificatory program. *Computer J.* **11:** 195.

Legendre, L., Legendre, P. (1983): *Numerical Ecology.* Elsevier, Amsterdam–Oxford–New York, 419. pp.

Podani, J. (1979): Association analysis based on the use of mutual information. *Acta Bot. Acad. Sci. Hung.* **25:** 125–130.

Podani, J. (1980): SYN-TAX: Computer program package for cluster analysis in ecology, phytosociology and taxonomy. *Abstracta Botanica* (Budapest) **6:** 1–158.

Podani, J. (1984): SYN-TAX II. Computer programs for data analysis in ecology and systematics. *Abstracta Botanica* **8:** 73–94.

Simon, T. (1977): *Vegetationsuntersuchungen im Zempléner-Gebirge* (Die Vegetation Ungarischer Landschaften 7.) Budapest, 350. pp.

Soó, R. (1963): Systematische Übersicht der pannonischen Pflanzengesellschaften. VI. Die Gebirgswälder. II. *Acta Bot. Acad. Sci. Hung.* **9:** 123–150.

Szujkó-Lacza, J. (1964): Die kalkholden und Eichen-Zerreichenwälder des Börzsöny-Gebirges. *Acta Bot. Acad. Sci. Hung.* **10:** 239–256.

Zólyomi, B. (1950): Fitostsenosy i lesomelioratsii obnashenih gor Budy (Les phytocenoses des montagnes de Buda et le reboisement des endroits dénudes. Russian, with French summary). *Acta Biol. Acad. Sci. Hung.* **1:** 367–430.
Zólyomi, B. (1958): Budapest és környékének természetes növénytakarója (Natural vegetation in Budapest and its environ). In: Pécsi, M. (ed.): *Budapest Természeti Képe* (*The Natural Features of Budapest*). 511–642.
Zólyomi, B. (1964): Methode zur ökologischen Charakterisierung der Vegetationseinheiten und zum Vergleich der Standorte. *Acta Bot. Acad. Sci. Hung.* **10:** 377–416.
Zólyomi, B., Jakucs, P., Baráth, Z., Horánszky, A. (1955): Forstwirtschaftliche Ergebnisse der geobotanischen Kartierung im Bükk-Gebirge. *Acta Bot. Acad. Sci. Hung.* **1:** 361–395.

Acta Botanica Hungarica 33 (1–2), pp. 41–49 (1987)

ECOLOGICAL OBSERVATIONS ON AQUATIC HYPHOMYCETES OF HUNGARY, III

J. GÖNCZÖL

HUNGARIAN NATURAL HISTORY MUSEUM, BOTANICAL DEPARTMENT,
P.O.B. 222, H-1476 BUDAPEST, HUNGARY

(Received: 1. May 1986)

Earlier studies on aquatic hyphomycetes of the Morgó stream system of the Börzsöny Mts. were continued and completed by investigations of some chemical characteristics of the stream. These investigations indicate that the distribution of the species communities is more influenced by the change of water chemistry than by the substratum preference. Control investigations on aquatic hyphomycetes of two softwater and two hardwater streams of Bükk Mts. confirmed the result obtained for the distribution of some species of the Morgó stream system.

Introduction

Preliminary comparative studies on aquatic hyphomycetes of the Bükk Mts. (Bükk National Park, NE-Hungary) made in the recent years have indicated that there is a distinct difference between the species composition and frequency of some species of the streams of the Bükk Mts. and the streams of the Börzsöny Mts., however, riparion vegetation of the studied streams of both mountains are very similar. At the same time, however, there were streams in the Bükk Mts. the species composition of the aquatic hyphomycetes of which were very similar to the species composition of the Morgó stream system of the Börzsöny Mts.

In the nineteen-seventies several observations were made on Ingoldian aquatic hyphomycete communities of a stream system of the Börzsöny Mts. (Northern Hungary). Two studies (GÖNCZÖL 1975, 1976) have dealt with several habitats of aquatic hyphomycetes in Hungary. Of these, in the earlier (GÖNCZÖL 1975) observations were reported on the longitudinal distribution pattern of the species communities of aquatic hyphomycetes of the Morgó stream system of the Börzsöny Mts. Conspicuous differences were found in the composition of species communities of two well distinguishable sections of the stream. The riparion vegetation of the stream also differed strictly: the banks of the lower course of the stream were overhung predominantly with trees of alder (*Alnus glutinosa*) whereas the upper course of the stream was lined by beech and hornbeam (*Fagus silvatica*, *Carpinus betulus*). The lower course of the stream was characterized by *Tetracladium marchalianum* and *Tricladium angulatum*, species predominantly present during the whole year on the one hand, as well as by the absence or very low frequency of *Dactylella aquatica* and *Monotosporella tuberculata* on the other. As opposed to these findings *Dactylella aquatica* and *Monotosporella tuberculata* were found to be a common species in the upper course of the stream (mainly in the winter months of the year) and vice versa the proportion of *Tetracladium marchalianum* and *Tricladium angulatum* were much more restricted. This longitudinal distribution pattern of some aquatic hyphomycetes of the Morgó stream system characterized by two species communities differring markedly in downstream direction, has frequently been observed and confirmed during the past decade. Distribution of *Dactylella aquatica* and even more of *Monotosporella tuberculata* being restricted to the upper course of the stream in the beech region, were attributed to the

available leaf substrate. Explanation for the restricted distribution of these species was based on the presumed phenomenon of the substrate preference of aquatic hyphomycetes. It appeared that the hypothesis of substratum specificity of aquatic hyphomycetes (or at least some of them) was confirmed by a good correlation found between the abundant occurrence of the "upper course species" (*Monotosporella tuberculata*, *Dactylella aquatica*, *Anguillospora crassa*) and their leaves substrate (*Fagus silvatica*, *Carpinus betulus*). Laboratory studies on the growth and sporulation of these species on their natural substrate supported to a great extent the conclusion drawn from the analysis of foam samples. Nevertheless discrepancies also occurred. A similarly good correlation between "lower course species" (*Tricladium angulatum* and *Tetracladium marchalianum*) and the predominant leaf substrate (*Alnus glutinosa*) of the lower course of the stream could not be found. A further discrepancy was that, although alder leaves were mixed with hornbeam at certain points of the lower course of the stream, *Monotosporella tuberculata* and *Dactylella aquatica* did not grow on them, while hornbeam-litter provided a suitable substrate for the same hyphomycete species on the upper course of the stream. This discrepancy in distributional behaviour of *Monotosporella tuberculata* was recognised in the case of *Quercus* leaves substrate, too, and was mentioned in a previous study (GÖNCZÖL 1975), but no explanation could be found for it.

The observations and results of BÄRLOCHER and co-workers on the distribution of aquatic hyphomycetes in softwater and hardwater streams, reported in several papers, have suggested that it is necessary to examine the chemical characteristics of the streams studied in Hungary. Also BÄRLOCHER and co-workers' recognition of the role of water chemistry in the distribution of aquatic hyphomycetes necessitated to re-examine the results of the earlier observations made on the distribution of aquatic hyphomycetes in the Morgó stream system of the Börzsöny Mts. (GÖNCZÖL 1971, 1975), as well as to complete these earlier observations with examinations of the chemical characteristics of the stream.

Therefore, the purpose of the present study was to investigate some chemical characteristics of the Morgó stream system, and to look for correlations between the longitudinal distribution pattern of the species communities, well known for many years, and the water chemistry of the stream. The other purpose was to look for a similar distribution pattern of aquatic hyphomycetes in other streams of Hungary, and especially, to look for the occurrence of *Monotosporella tuberculata* under different environmental conditions in other streams of Hungary. Some results and interpretations of the investigations of water chemistry of the Morgó stream system, as well as some results of the comparative studies made on some aquatic hyphomycetes of the Bükk Mts. are reported in this paper.

Materials and methods

Geographical, hydrological and geological description of the studied area but no chemical characteristics of the Morgó stream system were reported in previous papers (GÖNCZÖL 1971, 1975). Although investigations of pH values have continuously been made during the studies, these data were not recorded either.

During the recent study the total hardness of the water of the Morgó stream was investigated, started from the lower course of the stream and going towards the spring. A titration method was used to determinate the total hardness of the stream-water and values were given in German degrees. The determination of water hardness was made directly in the field, immediately after taking water samples from the stream. The investigated course of the Morgó stream extended to a cca. 20 km section of the stream and included almost the total length of the main branch of the stream. Water samples were taken at ten sampling sites at about 2 km distance. Also the pH value and water temperature were measured at each sampling site. Examinations of water quality were made in February 1986 and repeated in April 1986.

The Bükk Mts. are the most varied member of the Central Hungarian Range both from the geographical and geological aspect. It consists in a significant part of lime-containing sediment, as opposed to the Börzsöny Mts., where limestone is almost completely absent from the surface forming rock. Four streams of the Bükk Mts. in the area of the Bükk National Park were selected for comparative studies on the structure of aquatic hyphomycete communities as well as for detecting the presence or absence of some species known to show a restricted distribution in the Morgó stream. Of the four streams two (Sebesvíz stream and Kőlyuk stream) with hardwater, and the two others (Pénz stream and Rejteki stream) with softwater, were examined (Table 1).

Table 1

Some chemical characteristics of the five streams studied

	Bükk Mts.				Börzsöny Mts.	
	I	II	III	IV	V/a	V/b
pH	5	4.9	6.2	5.8	5.8	5
Total hardness	4–5	3–4	14–15	17–18	9–10	3–4

I. Rejtek stream, II. Pénz stream, III. Sebesvíz stream, IV. Kőlyuk stream, V/a Morgó stream (lower course), V/b Morgó stream (upper course).

The beds of the hardwater streams consist of mesozoic clayey calcareous schist and paleosoic clayey pebbly limestone, whereas the beds of the softwater streams consist of siliceous schist and pebbly-clayey shale.

The riparian vegetation of the two hardwater streams were very similar to each other as well as to that of the upper course of Morgó stream in the Börzsöny Mts., i.e. the input of leaf substrate derived from beech trees (*Fagus silvatica*). In addition to this, *Acer pseudoplatanus* and *Carpinus betulus* contributed in a significant part to the available leaf substrate in the streams. The riparion vegetation of the two softwater streams, too, consisted of beech, hornbeam and maple (*Fagus silvatica, Carpinus betulus, Acer* spp.) but smaller mixed stands of *Picea abies* chequered this woody vegetation in some place.

Foam samples and decaying leaf samples have been collected since 1984. The selected streams were investigated in all four seasons, at least on one occasion. Samples were taken usually in March, May or June, October and December.

The frequency of the species was estimated from foam samples collected usually from two or three km sections of the streams. Estimations were based on the analysis of the spore content of ten drops (cca. 0.5 ml) of foam samples. For calculation of the conidial number was used low magnification of microscope (16×10). The following three proportions of occurrence were used to detect the frequencies of individual species.

Common: one or some conidia are encountered at least, in each visual fields of the observed drop of foam sample.

Sparse: regularly encountered one or some conidia at least in the half number of the visual fields.

Rare: not more than one or some conidia are encountered in a full drop of the foam sample observed.

More detailed description of the method of foam sample analysis and of the investigation of leaf samples is given in some previous papers (Gönczöl 1971, 1975, Gönczöl and Révay 1983). As it is a well-known fact foam sample analysis is unsuitable for the exact quantification of aquatic hyphomycetes of a certain stream but if foam sample analysis is completed with simultaneous investigation of leaf samples, the two methods yield reliable data on the presence or absence of individual species and on the tendency of the distribution of the species communities.

Results and discussion

Determination of the total hardness of the Morgó stream water over a cca. 20 km distance of the stream yielded a very slight but constant decrease of the values of total hardness in upstream direction. At the first sampling site, near the mouth of the stream, the water hardness was 9–10 (in German degrees) whereas at the highest sampling point of the stream near the spring, it was only three degrees. A slight gradual decrease of the values was observed at the intermediate sampling sites (Fig. 1).

The longitudinal pattern of the total hardness of the water of the Morgó stream exhibits a noteworthy correlation with the longitudinal distribution pattern of so-called "upper course species" and "lower course species". Namely, the species known as "upper course species" (*Monotosporella tuberculata, Dactylella aquatica* and *Anguillospora crassa*) commonly distributed in the upper course of the Morgó stream, are actually restricted to the softwater section (3–5 degrees of total hardness) of the stream. *Monotosporella tuberculata* exhibits most markedly this restriction, but a similar restricted distribution characterizes *Dactylella aquatica, Anguillospora crassa, Tricladium splendens* and *Articulospora tetracladia*, too. All these species occur in the lower course of the stream (total hardness 9–10 degrees) with considerably lower percentage in the conidial pool.

A similarly good correlation may be recognized between the longitudinal distribution pattern of so-called "lower course species" and the harder (9–10 degrees) water of the lower course of the stream. *Tetracladium marchalianum* exhibited, in this regard, the most clearcut correlation with its abundant occurrence in this section of the stream, and, at the same time, with its almost total absence in the upper course of the stream. This finding agrees with that of BÄRLOCHER and ROSSET (1981) who found *Tetracladium marchalianum* to

Degrees of total hardness
0 1 2 3 4 5 6 7 8 9 10
Upstream
0 5 10 15 20
Stream length (km)

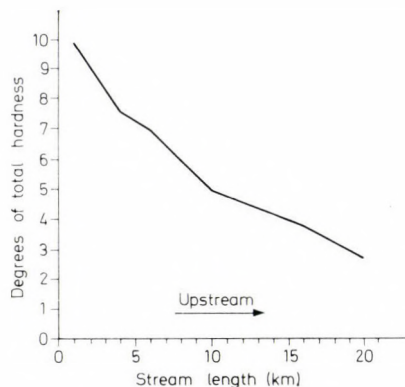



Fig. 1. Change of the values of total hardness in the water of Morgó stream

be a characteristic hardwater species. Although the water of the lower course of the Morgó stream is not typical hardwater, the value of the total hardness of its water is three times higher than the value of total hardness obtained for the upper course of the stream, consequently this difference may cause the regression of some sensitive species and the progression of more tolerant species.

Conidia of another characteristic "lower course species", *Tricladium angulatum*, occurred in foam samples of the upper course of the stream too, but not nearly as abundantly as in foam samples obtained from the lower course of the stream.

No clearcut correlation could be observed between the change of water hardness and distribution pattern of *Alatospora* species (*A. acuminata, A. flagellata*) of the Morgó stream. *Alatospora acuminata* showed almost the same frequencies of occurrence in any part of the stream and appeared to be rather an indifferent (similarly to *Clavariopsis aquatica* and *Heliscus lugdunensis*) than a characteristic hardwater species. *Alatospora flagellata* could also be found in any foam samples of the stream, but its growth and sporulation could only be observed on the leaf substrate taken from the upper course of the stream.

With the knowledge of water hardness of the Morgó stream, frequencies of occurrence of some species in this stream show a good coincidence with Bärlocher's findings obtained for the occurrence of the same species in softwater and hardwater streams. They consider *Tricladium splendens* and *Articulospora tetracladia* to be typical softwater, whereas *Alatospora acuminata*, *Tricladium angulatum* and *Tetracladium marchalianum* to be typical hardwater species (Rosset and Bärlocher 1985a, 1985b). The same species studied in the Morgó stream show a very similar phenomenon but not by their distribution in two different types of streams (softwater and hardwater) but in the same stream, too, according to the changes of the total hardness of the stream water.

Since in the Morgó stream system of the Börzsöny Mts. *Monotosporella tuberculata* most distinctly exhibited the restricted distribution, this species appeared to be one of the most suitable species to investigate its correlation with water hardness of the streams of the Bükk Mts. As it is given in Table 2, *Monotosporella tuberculata* showed a very similar distribution to that of its pattern in the Morgó stream, namely, its conidia occurred with high frequency in the samples of the two softwater streams, whereas very few conidia (fully absent in some samples) could be encountered with in the samples of the two hardwater streams. It is interesting to note: that there was little difference in conidial frequency of *Monotosporella tuberculata* in foam samples of the two hardwater streams. Namely, whereas conidia of *M. tuberculata* were practically absent from foam samples of the Sebesvíz stream, some of them could be encountered in the other hardwater stream (Kőlyuk stream), although a

Table 2

Frequency of occurrence of hyphomycete species collected from the four streams of the Bükk Mts.

	I	II	III	IV
Actinospora megalospora Ingold	✳			
Alatospora acuminata Ingold	✳	□	□	□
Alatospora flagellata (Gönczöl) Marv.	✳	○	□	○
Anguillospora crassa Ingold	□	□	○	○
Anguillospora longissima (Sacc. et Syd.) Ingold	□	□	□	□
Angulospora aquatica Nilsson (?)			○	✳
Articulospora tetracladia Ingold	□	○		
Bacillispora aquatica Nilsson	○	○	✳	
Clavariopsis aquatica de Wildeman	□	○	✳	✳
Clavatospora longibrachiata (Ingold) Nils. ex Marv. et Nils.		□		
Culicidospora gravida Petersen	○	✳	✳	○
Cylindrotrichum helisciforme Marv.		✳	○	✳
Dactylella aquatica (Ingold) Ranzoni	□	□	✳	✳
Diplocladiella scalaroides Arnaud			✳	✳
Dwayangaam cornuta Descals et Webster	✳			
Flagellospora curvula Ingold	○	✳	○	○
Geniculospora inflata (Ingold) Nils. ex Marv. et Nils.		✳		
Heliscella stellata (Ingold et Cox) Marv.	○	□		○
Heliscus lugdunensis Sacc. et Théry	✳	○	✳	○
Isthmotricladia britannica Descals		✳		
Lemonniera aquatica de Wildeman	□	□	✳	✳
Lemonniera terrestris Tubaki	○	□	✳	
Margaritispora aquatica Ingold	✳			
Monotosporella tuberculata Gönczöl	□	□	✳	✳
Mycocentrospora aquatica (Iqbal) Iqbal			○	○
Mycocentrospora sp. (*clavata* ?)			□	□
Tetracladium marchalianum de Wildeman	✳	○	✳	○
Tetracladium maxilliforme (Rostrup) Ingold		✳		
Tetracladium setigerum (Grove) Ingold	✳	○		
Tricladium angulatum Ingold		✳	✳	□
Tricladium gracile Ingold	○	□		
Tricladium splendens Ingold	□	□		
Tricladium sp.			□	○
Triscelophorus sp.	✳		✳	✳
Vargamyces aquatica (Dudka) Tóth			○	○
Varicosporium elodeae Kegel		✳		
Unknown sigmoid conidia			□	□

□ = common, ○ = sparse, ✳ = rare
I = Rejtek stream, II = Pénz stream, III = Sebesvíz stream, IV = Kőlyuk stream

somewhat higher value of total hardness (with 3–4 degrees) of this latter stream was found. It may probably be noteworthy that the pH value of this latter stream was somewhat lower.

There are some data in the literature on the occurrence of this species. It is interesting that during a comparative study of aquatic hyphomycetes of softwater and hardwater streams of the Black Forest and the Swiss Jura,

Monotosporella tuberculata was determined from one of the two hardwater streams of the Swiss Jura, whereas it was fully absent in the two softwater streams of the Black Forest (BÄRLOCHER and ROSSET 1981).

If the pH values of the two Black Forest streams are compared with the pH values of the softwater streams of the Börzsöny Mts. or the Bükk Mts., considerably higher pH values can be found at Ibach and Schwarzenbächle (pH 7.28 and 6.49) than those of the investigated Hungarian streams (pH 4.9–5).

The abundant occurrence of this species in some Hungarian streams as well as the absence in the mentioned Black Forest streams suggests that softwater and slightly acidic pH are equally needed for the optimal growth of *Monotosporella tuberculata*, and the absence of any of these physiological requirements apparently inhibits the distribution of this species. On the other hand, another study of BÄRLOCHER and WOOD-EGGENSCHWILER does not support this consequence because they found *Monotosporella tuberculata* to be almost equally distributed both in the softwater and hardwater streams of the Black Forest, Vosges, Jura and Napf, although only the presence and absence of the investigated species were considered (WOOD-EGGENSCHWILER and BÄRLOCHER 1983).

The distribution behaviour of *Tricladium angulatum* observed in the Morgó stream could only partly be confirmed, since it occurred with distinctly higher frequency only in one of the investigated two hardwater streams of the Bükk Mts. As it was pointed out *Tricladium angulatum* showed a fairly good correlation with hardwater in the Morgó stream, very similar to that of *Tetracladium marchalianum*. Also, well noticeable differences can be recognized between data recorded by BÄRLOCHER, where definitely higher frequencies of occurrence of this species are shown in the two hardwater streams than in the two softwater streams (BÄRLOCHER and ROSSET 1981).

Few species were encountered during this study in the Bükk Mts. which were characteristic solely for the hardwater streams. As it is given in Table 2, only a *Tricladium* species was commonly seen in foam samples derived from the two hardwater streams and could not be demonstrated in softwater stream at all. Again, a *Mycocentrospora* species (closely related to *M. clavata*) appeared to be widely distributed but predominantly in the hardwater streams of the Bükk Mts. Up till now, these species have been unexplored among aquatic hyphomyces of Hungary and seem to be absent from the conidial pools of the investigated streams of the Börzsöny Mts.

In this respect the present investigations on some streams of the Bükk Mts. do seem not to confirm the observation of BÄRLOCHER and ROSSET: "all fungi found in the hardwater streams are also present in softwater", but definitely confirm their other observation: "there are some species restricted to softwater streams" (ROSSET and BÄRLOCHER 1985b).

Little evidence has so far been obtained on the softwater and hard-

water streams of the Bükk Mts. to confirm or contradict BÄRLOCHER's observation suggesting that there is "a striking difference in fungal species richness between hardwater and sofrwater streams, with twice as many species in the softwater streams" (ROSSET and BÄRLOCHER 1985a). Unfortunately, the total species richness of the four studied streams could not be compared because some of the studied species in both types of streams remained unidentified or only doubtfully identified. It is interesting, however, that if the total number of the fully identified species of the softwater and hardwater streams are compared, the similar striking difference in species richness observed by BÄRLOCHER could not be obtained, though some species could only just be demonstrated in the samples of the two hardwater streams (see Table 2). One of the two softwater streams (Pénz stream) has the highest species number (with 26 species) but the species number (with 24 species) found in one of the two hardwater streams (Sebesvíz stream) was hardly lower. Thus the main difference seems to be more in the frequencies of occurrence than in the species richness of the hardwater and softwater streams studied in this area.

A number of problems connected with the methods of investigating aquatic hyphomycetes (e.g. filtration technique, foam sample analysis) have been encountered and pointed out in papers published in recent years (SHEARER and LANE 1983, SHEARER and WEBSTER 1985). Thus, only some careful and limited conclusions may be drawn. The present investigations were actuated by the results of BÄRLOCHER and made in the hope of finding correlations between the longitudinal distribution pattern of some aquatic hyphomycete species of the Morgó stream and some chemical characteristics of the stream. Some results of these chemical investigations make questionable the decisive significance of substratum preference in the distribution and restriction of the species communities in the Morgó stream as supposed earlier, and seem to confirm BÄRLOCHER's results according to which the water chemistry has a more significant role in the frequency of occurrence of some species than the substratum preference has. In this regard *Monotosporella tuberculata* is definitely influenced by water hardness (and probably by the pH) and appears to be a typical softwater species. Control investigations made in two softwater and two hardwater streams in a geologically different region of Hungary, gave a result very similar to that obtained for the Morgó stream of the Börzsöny Mts. At the same time, however, the present investigations, too, suggest that distribution of aquatic hyphomycetes may be strongly restricted by water hardness, not only in different streams, but in the same stream, too. The chemical characteristics of the streams may also considerably change. Gradual changes of water chemistry over a fairly long distance of a stream may be so significant that it may cause the same differences in the frequency of occurrence which exist in several streams differing in their water chemistry.

ACKNOWLEDGEMENTS

The author is grateful to Dr. GY. SZAKMÁNY (Petrological and Geochemical Department of Eötvös Loránd University, Budapest) for the petrographic determination of the investigated area of the Bükk Mts.

REFERENCES

Bärlocher, F., Rosset, J. (1981): Aquatic hyphomycete spora of two Black Forest and two Swiss Jura streams. *Trans. Br. mycol. Soc.* **76:** 479–483.

Gönczöl, J. (1971): Aquatic hyphomycetes from the Börzsöny. Mts. *Annls. hist.-nat. Mus. natn. hung.* **63:** 57–75.

Gönczöl, J. (1975): Ecological observations on the aquatic hyphomycetes of Hungary, I. *Acta Bot. Hung.* **21:** 243–264.

Gönczöl, J. (1976): Ecological observations on the aquatic hyphomycetes, II. *Acta Bot. Hung.* **22:** 51–60.

Gönczöl, J., Révay, Á. (1983): Observations on the hyphomycetes inhabiting forest litter of Hungary. *Acta Bot. Hung.* **29:** 107–125.

Rosset, J., Bärlocher, F. (1985*a*): Transplant experiments with aquatic hyphomycetes. *Verh. Internat. Verein. Limnol.* **22:** 2786–2790.

Rosset, J., Bärlocher, F. (1985*b*): Aquatic hyphomycetes: influence of pH, Ca^{2+} and HCO_3^- on growth in vitro. *Trans. Br. mycol. Soc.* **84:** 137–145.

Shearer, C. A., Lane, L. C. (1983): Comparison of three techniques for the study of aquatic hyphomycete communities. *Mycologia* **75:** 498–508.

Shearer, C. A., Webster, J. (1985): Aquatic hyphomycete communities in the River Teigh. III. Comparison of sampling techniques. *Trans. Br. Mycol. Soc.* **84:** 509–518.

Wood-Eggenschwiler, S., Bärlocher, F. (1983): Aquatic hyphomycetes in sixteen streams in France, Germany and Switzerland. *Trans. Br. Mycol. Soc.* **81:** 371–379.

Acta Botanica Hungarica 33 (1–2), pp. 51–58 (1987)

THE EFFECT OF SO_2, SO_3^{2-} AND SO_4^{2-} TREATMENT ON PHOTOSYNTHESIS AND CHLOROPHYLL CONTENT IN PROTONEMA OF *FUNARIA HYGROMETRICA*

J. KRUPA, E. TLAŁKA

INSTITUTE OF BIOLOGY, HIGHER PEDAGOGICAL SCHOOL,
PODBRZEZIE 3, 31-054 KRAKOW, POLAND

(Received: 15 January 1986)

The effect of SO_2, SO_3^{2-} and SO_4^{2-} on photosynthetic intensity and chlorophyll content in protonema of *Funaria hygrometrica* is studied. Direct action of the investigated substances on plant cells can be easily examined owing to the simple structure and close association of this developmental stage of mosses with water. Sulphur dioxide and sulphite ions act particularly toxically on photosynthesis while the concentration of chlorophyll is influenced by these sulphur compounds to a less degree. Protonema obtained from spores collected in an environment free of industrial pollution are much more sensitive to oxygen sulphur compounds than those from spores grown up under conditions of massive industrial pollution. The resistance to gas pollution of the air is then of a feature of plants growing in these conditions; it appears before the formation of spores.

Introduction

The ontogenesis of mosses consists of three stages which differ in their morphology and physiological requirements. In many respects the first stage of protonema resembles algae. The process of spore germination and growth of protonema as well as further developmental stages are closely connected with water (KRUPA 1964).

Mosses are classified to plants sensitive to industrial pollution, particularly that of sulphur dioxide (GILBERT 1968; INGLIS and HILL 1974; FERGUSON and LEE 1979). The particular sensitivity can be associated with a close dependence of these plants upon water. Sulphur dioxide is easily and in large amounts soluble in water. Also the changes of this gas to SO_3^{2-} and SO_4^{2-} are connected with availability of water (MUDD 1975). On the other hand, owing to their small sizes Bryophyta are in a fairly close contact with the soil solution. The buffering capacity of the soil solution can to a certain degree eliminate the toxic action of sulphur compounds connected with changes in pH. Some moss species, as *Funarica hygrometrica*, are observed in habitats strongly degraded by the action of industrial pollution. Another reason of tolerance to industrial pollution is the ability of these plants to produce mechanism which make possible their vegetation under the changed conditions. These mechanisms of resistance to SO_2 has not been clearly defined yet. They can be associated with the buffering capacity of cells of these plants. The occurrence of a moss species in the given area is connected with conditions which afford possibilities for the development of its successive stages. The literature data which stress the sensitivity of mosses are to a certain degree inconsistent with observations which show that sometimes these are the only plants appearing in areas strongly degraded by industrial pollution. Therefore, it can be assumed that either some species of mosses are much more tolerant or they produce certain abilities of adapting to these conditions. The examination of physiological effects of sulphur dioxide, and sulphite and sulphate ions on the moss species *Funaria hygrometrica* was the aim of present study.

Material and methods

The plant material used in experiments was collected in two habitats differing by the degree of industrial pollution. One lies in the nearest vicinity of the Lenin Metallurgic Plant, on spoil heaps of blast-furnace slag. The grounds were settled only by mosses, chiefly of the genus *Bryum*. In wetter places the species *Funaria hygrometrica* formed permanent communities. The average daily SO_2 concentration in air was 0.35–0.78 mg · m^{-3}. Besides, the emissions released by the plant contained great amounts of other pollution, above all flue dusts (GRODZIŃSKA 1980).

Another sampling station was established in a distance of 100 km south of Kraków and it was practically free of industrial pollution. *Funaria hygrometrica* plants grew on a well-insolated clearing covered with grass. Mature capsules were harvested in the two habitats in July 1978 and kept at room temperature and humidity. Spores were poured into glass container, their number being sufficient for all experiments. They were transferred with a sterile brush on Petri dishes, 10 cm in diameter, filled with 30 cm^3 of the Mohr medium. The dishes with spores were incubated at a constant temperature of 25 °C at 12-hour day regime, with the light intensity of 80 W · m^{-2}. The light sources were two LRFR lamps of 250 W and one tungsten bulb of 200 W. After 84 hours germinating spores were condensed by centrifugation at low rotation speed during 10 min.

Sulphur dioxide was obtained from the reaction of mercury and condensed sulphuric acid at increased temperature. The necessary concentration was obtained by its gradual dilution with dried air.

The dishes with protonema were placed in a tight glass vessel 10 dm^3 in volume and measured amounts of gas were introduced there to obtain SO_2 concentration of 0.3, 3, 5 and 10 mg · m^{-3}. The exposure to SO_2 took 12 hours and was carried out in the dark. Sulphite and sulphate ions in the form of sodium salts solutions were added in the amount of 1 cm^3 per 10 cm^3 of the medium. The concentration of ions was 3, 9, 15 and 30 mMol in the different runs of experiments. Protonema were exposed to the given substance during 12 hours in the dark.

The concentration of SO_2 in air was checked using the West and Gaeke method (1956). The rate of oxidation of sulphite to sulphate was determined by gravimetric analysis.

The intensity of photosynthesis in *Funaria hygrometrica* protonema was measured using a microrespirometer method (ZURZYCKI 1955, 70, STARZECKI 1961), at the intensity of white light exceeding the saturation point which was experimentally determined (Fig. 1). In the gaseous phase the concentration of CO_2 was 0.3% and it was obtained by using Warburg buffer at concentration 0.2 mol (ZURZYCKI 1970). The intensity of respiration was measured in the dark. The protonema culture and measurements of gas exchange were carried out at 25 °C. Chlorphyll content in protonema was determined using the method described by GOODWIN (1965) and calculated according to the MACLACHLAN and ZALIK formula (1963). Chlorophyll concentration was expressed in mg · g dry $weight^{-1}$. Dry weight was found on the basis of the previously determined water content in protonema. Averaged results are based on 6–8 replications of measurements of gas exchange and chlorophyll content. The obtained results were statistically evaluated, the STUDENT–GOSSET test being employed.

Results

In *Funaria hygrometrica* grown up from spores collected in the area free of industrial pollution (station A) net photosynthesis was 7.45 mm^3 · 10 min^{-1} · $mgdw^{-1}$, while the photosynthetic intensity of protonema obtained from spores harvested in the ground of the metallurgic plant (station B) was almost 2.5 times lower: 2.98 mm^3 · 10 min^{-1} · $mgdw^{-1}$.

The process of spore germination and growth of protonema occur in aquatic environments. Dependences connected with SO_2 solubility in water being taken into consideration, the concentration found in the direct neighbourhood of the plant cell is most significant in determining the influence of the gas on it. In the present paper data on SO_2 occurrence refer to the concentration of this gas in the liquid phase to which the protonema were exposed. Differences in SO_2 concentration in air and in water are fairly significant since at the content of this gas in air reaching 10 mg · m^{-3}, the experimentally measured amount of SO_2 in water was 1.40 mg · cm^{-3} under conditions of the investigation.

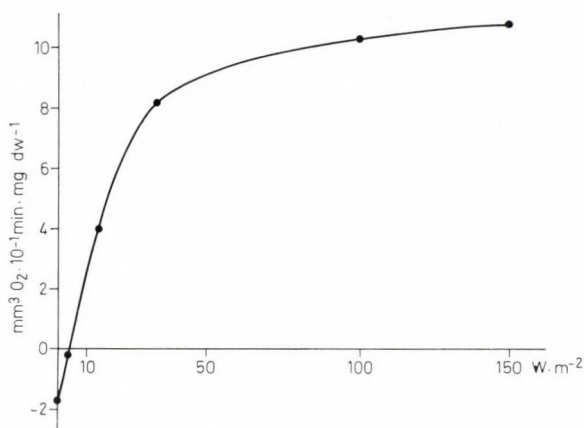



Fig. 1. The effect of radiation intensity on the rate of net photosynthesis in the protonema of *Funaria hygrometrica*

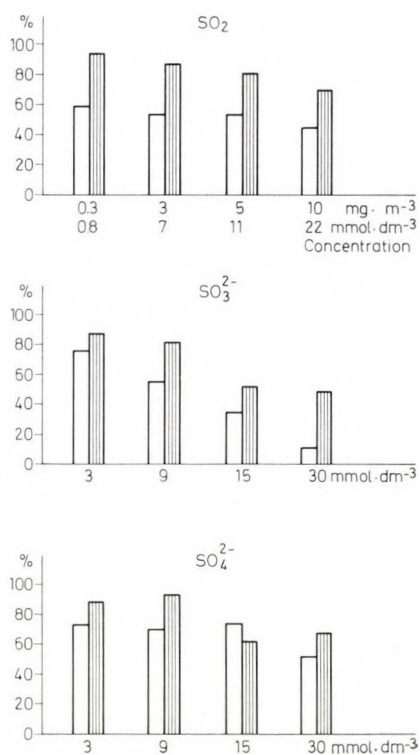



Fig. 2. Relative net photosynthesis rate in the protonema of *Funaria hygrometrica* at various concentrations of SO_2, SO_3^{2-}, SO_4^{2-}. Time of treatment 12 hours. □ — material from unpolluted habitat, ▥ — material from polluted habitat

In protonema treated with SO_2 during 12 hours in the dark phase a depression of photosynthesis was observed. In spite of fairly distinct differences in the concentration of SO_2, its effect on the photosynthetic process was hardly differentiated. Protonema grown of spores from station A showed the photosynthetic intensity lower by 50% on the average, as compared with those grown under control conditions, while protonema obtained from spores maturating in the grounds of the metallurgic plant showed a 20% drop in photosynthesis (Fig. 2).

The reaction of the Mohr culture medium is acid with the pH of 5.5. During germination of spores and growth of protonema pH changed to 7.4 and was maintained at this level for a longer time. The value of pH of the medium increased to 8.8 at the highest concentration of sodium sulphite. After 12-hour treatment of the plant material under these conditions, pH of the solution changed to 8.1. With lower concentrations of sulphite ions, pH of the medium was 7.9–7.3 during this period.

The protonema of *Funaria hygrometrica* treated with SO_3^{2-} ions during 12 hours showed a distinct inhibition of photosynthesis, the inhibition effect being dependent upon the concentration of these ions (Fig. 2). A slight (20%) decrease in photosynthesis appeared under the influence of SO_3^{2-} at the concentration of 3 mmol. In protonema A incubated in the medium containing 30 mmol SO_3^{2-} photosynthesis was almost completely inhibited. All sulphite concentrations brought about distinctly less inhibition of photosynthesis in protonema obtained from spores harvested at station B.

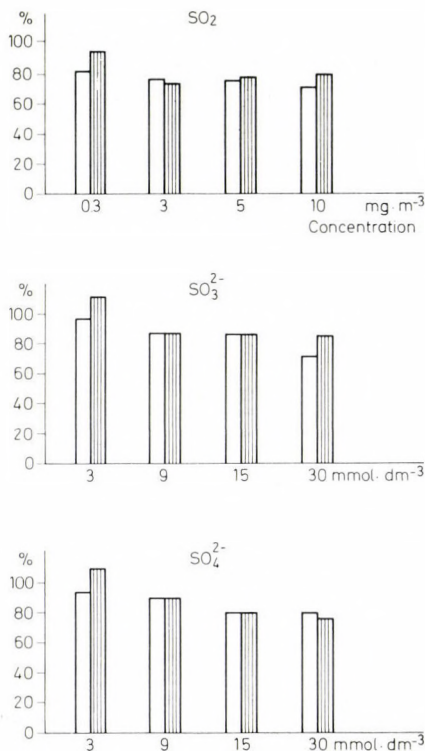



Fig. 3. Relative content of chlorophyll a + b in the protonema of *Funaria hygrometrica* treated with various concentrations of SO_2, SO_3^{2-}, SO_4^{2-}. Description as in Fig. 2

The toxicity of sulphate ions to photosynthesis is evidently lower than that of ions discussed above, being more pronounced in protonema grown up from spores from station A. Photosynthesis of these protonema exposed to sulphate at the concentrations of 30 mmol was reduced by almost 50% as compared with the control. Under the influence of other concentrations the drop in the photosynthetic intensity was between 20–40% of the control value, no decided dependence upon the concentration of the applied compound being observed.

As it was frequently found sulphur oxygen compounds induce changes in chlorophyll concentration. This was particularly distinct under conditions of a pronounced acidification of the cell inside. The sulphur compounds and their concentrations employed in the study do not effect such significant changes, therefore the changes in the concentration of chlorophyll in protonema exposed to SO_2, SO_3^{2-} and SO_4^{2-} during 12 hours were slight. In protonema treated with the investigated compounds decrease in chlorophyll content did not exceed 30% of the control value and was found when the highest concentrations were applied. In case of other concentrations a decrease in chlorophyll content was lower than 20%, neither was there any distinct difference between protonema grown up from spores collected at stations characterized by different degrees of degeneration brought about by industrial pollution (Fig. 3).

Discussion

As the criteria of the quantitative evaluation of SO_2 toxicity, changes in the photosynthetic uptake of CO_2 or oxygen evolution are most frequently used. Among other factors, the drop in CO_2 uptake is explained by changes in the activity of enzymes, above all of RuDP and PEP carboxylase, however, there is no agreement on the subject of mechanisms of this effect (Ziegler 1972, Gezelius and Hälgren 1980).

On the other hand, the inhibition in oxygen evolution observed under the influence of SO_2 is probably caused by disorganization of light reactions of photosynthesis connected with the photosystem II (Shimazaki and Sugahara 1979, 1980). Also the damages of chloroplasts can be responsible for changes in the photosynthetic intensity under the influence of the discussed constituent of gaseous air pollution (Fischer et al. 1973, Młodzianowski and Białobok 1976, Godzik 1976, Wong et al. 1977).

Most investigations on the effect of industrial pollution on mosses dealt with its influence on gametophores. The complex cycle of moss development being taken into consideration, the occurrence of these plants in the given area depends upon the reaction of the different development stages to pollution. On the other hand, various levels of organization in the individual stages of alternation of moss generations make it possible to study a wider spectrum of dependences in the action of pollution on plants.

Protonema of mosses are particularly sensitive to SO_2 if the toxic action of this gas is measured by changes in the photosynthetic intensity. At SO_2 concentration in the gaseous phase of 10 $mg \cdot m^{-3}$, oxygen evolution by protonema incubated in a solution containing 22 mmol $SO_2 \cdot dm^{-3}$ was reduced to almost 50% of the control value. This high inhibition was found in

protonema grown up from spores maturing in the habitat free of industrial pollution. In the culture of spores from the outskirts of the metallurgic plant protonema showed markedly lower sensitivity and under the same conditions their photosynthesis was reduced by 30%. When protonema were treated with SO_2 of 0.3 mg · m^{-3} concentration in air, the drop in photosynthesis was 6% only. This concentration only slightly differs from daily concentrations permitted by the Polish Norms. Though, the daily concentration of SO_2 in the vicinity of station B was about 0.8 mg · m^{-3}. These data distinctly suggest that differences in the sensitivity of protonema depend upon conditions of spore production. The observed differentiation indicates that the adaptation ability appears already in the spore. Owing to lack of more comprehensive data, it is difficult to define the character of differences in the sensitivity to SO_2, the more so that under conditions of the control the photosynthetic intensity of protonema from the slag dumping grounds was almost half of that found in protonema grown up from spores which matured in habitat A. These results indicate that the growth of protonema and their further development are possible even under conditions of relatively high SO_2 concentration in air. However, the toxicity of this gas is evident and can be distinctly observed in plants growing in areas free of industrial pollution.

The toxic effect of sulphite on photosynthesis of *Funaria* protonema was also observed. The inhibition of photosynthesis by sulphite was even stronger than in case of SO_2 treatments. In the range of higher concentration of these compounds the inhibition could reach 90% in protonema obtained from spores from habitat A. Also in this case differences in the reaction of protonema produced by spores from different conditions of atmospheric pollution could be observed. Differences in the inhibition of photosynthesis were particularly distinct at higher concentrations of sulphite used in the treatment of protonema.

The toxicity of sulphite depends upon the pH of the medium. In an acid solution predominates the HSO_3^- form, while with the pH lower than 2 exists undissociated sulphurous acid (GILBERT 1968, PUCKETT et al. 1973). However, in numerous works these are rather theoretical discussions because of difficulties in discerning the influence of pH from the effect of sulphite on the investigated process. The inhibition of this process during long term treatments can be associated with the appearance of SO_4^{2-} ions. As it was found, the rate of these changes depends on the concentration of sulphite ions. Sulphate is a sort of natural sulphur compound for plants and its toxicity was not noted when appeared at low concentrations (HILL 1974, FERGUSON and LEE 1979). However, an increase in the concentration of sulphate ions in the cell can disturb its physiological processes, analogically to the action of sulphite (GILBERT 1968, FERGUSON et al. 1978).

Under natural conditions the toxicity of sulphur dioxide is also observed when, in the form of sulphuric acid, it is removed from the atmosphere with

rains. When the concentration of sulphur in the rainwater is relatively high, the damage to the chlorophyll appears first (SHERIDAN and ROSENTRETER 1973, GODZIK 1976). However, the pheophytinization of chlorophyll caused by SO_2 (RAO and LEBLANC 1966, NASH 1973) occurs when the pH of the outer solution is lower than 3 (PUCKETT et al. 1973), though changes in chlorophyll concentration were also observed when the pH of the environment was less acid (MALHOTRA 1977, SOLDATINI et al. 1978).

The results suggest the possibility that there occurs another mechanism of destructive action of sulphur compounds on chlorophyll. The drop in chlorophyll concentration of protonema exposed to sulphur compounds does not exceed the inhibition of photosynthesis. A decrease in chlorophyll content did not exceed 30% of the initial value and was chiefly noted in protonema grown up from spores maturing at habitat A. The complexity of sulphur dioxide conversions and multidirectional influences affecting the processes inside the cell being taken into consideration, the observed effect on photosynthesis can be a resultant of this dependence.

ACKNOWLEDGEMENTS

This work was partially supported by Polish Academy of Science with the project 5.4.3.

REFERENCES

Ferguson, P., Lee, J. A., Bell, J. N. B. (1978): Effects of sulphur pollutants on the growth of Sphagnum species. *Environm. Pollut.* **16:** 151–155.

Ferguson, P., Lee, J. A. (1979): The effects of bisulphite and sulphate upon photosynthesis in Sphagnum. *New Phytol.* **83:** 703–712.

Fischer, K., Kramer, D., Ziegler, H. (1973): Elektronenmikroskopische Untersuchungen SO_2-begaster Blätter von *Vicia faba*. *Protoplasma* **76:** 83–96.

Gezelius, K., Hällgren, J-E. (1980): Effects of SO_3^{2-} on the action of ribulose biphosphate carboxylase from seedlings of Pinum silvestris. *Physiol. Plant.* **49:** 354–358.

Gilbert, O. L. (1968): Bryophytes as indicators of air pollution in the Tyne Valley. *New Phytol.* **67:** 15–30.

Godzik, S., Piskornik, Z. (1969): Oddziaływanie zanieczyszczeń powietrza na rośliny. I. Żródła i rodzaje zanieczyszczeń powietrza oraz formy uszkodzeń roślinności. *Wiad. Bot.* **13:** 239–248.

Godzik, S. (1976): Pobieranie $^{35}SO_2$ z powietrza i rozmieszczenie ^{35}S u niektórych gatunków drzew. *Wyd. PAN.*

Goodwin, T. (1965): *Chemistry of Plant Pigments.* Acad. Press London, pp. 462–485.

Grodzińska, K. (1980): Acidification of forest environment (Niepołomice Forest) caused by SO_2 emission from steel mills. *Final report 1976–80, Cracow.*

Hill, D. J. (1971): Experimental study of the effect of sulfite on lichens with reference to atmospheric pollution. *New Phytol.* **73:** 1207–1213.

Krupa, J. (1964): Studies on the physiology of germination of spores of *Funaria hygrometrica* Sibth. I. *Acta Soc. Bot. Pol.* **33:** 179–192.

Malhotra, S. S. (1977): Effects of aqueous sulphur dioxide on chlorophyll destruction in Pinus contorta. *New Phytol.* **78:** 101–109.

Maclachlan, S., Zalik, S. (1963): In: *Chemistry of Plant Pigments.* Goodwin T. W. Acad. Press London 1965.

Młodzianowski, F., Białobok, S. (1977): The effect of sulphur dioxide on ultrastructural organization of lark needles. *Acta Soc. Bot. Pol.* **46:** 629–634.

Mudd, J. B. (1975): Sulfur dioxide. In: *Responses of Plants to Air Pollution.* Acad. Press N.Y., San Francisco, London. pp. 9–22.
Nash, T. H. (1973): Sensitivity of lichens to sulphur dioxide. *Bryologist* **76:** 333–339.
Piskornik, Z., Godzik, S. (1970): Oddziaływanie zanieczyszczeń powietrza na rośliny. II. *Wiad. Bot.* **2:** 91–102.
Puckett, K. J., Nieboer, E., Flora, W. P., Richardson, D. H. S. (1973:) Sulphur dioxide: its effects on photosynthetic $^{14}CO_2$ fixation in Lichens and suggested mechanisms of phytotoxicity. *New Phytol.* **72:** 141–154.
Rao, D. N., LeBlanc, F. (1966): Effects of sulfur dioxide on the lichen algae, with special reference to chlorophyll. *Bryologist* **69:** 69–75.
Sheridan, R. P., Rosentreter, R. (1973): The effect of hydrogen ion concentration in simulated acid rain on the moss Tortura ruralis (Hedw.). *Bryologist* **76:** 168–174.
Shimazaki, K., Sugahara, K. (1979): Specific inhibition of photosystem II activity in chloroplasts by fumigation of spinach leaves with SO_2. *Plant Cell Physiol.* **20:** 947–955.
Shimazaki, K., Sugahara, K. (1980:) Inhibition site of the electron transport system in lettuce chloroplasts by fumigation of leaves with SO_2. *Plant Cell Physiol.* **21:** 125–135.
Soldatini, G. F., Ziegler, I., Ziegler, H. (1978): Sulfite: Preferential sulfur source and modifier of CO_2 fixation in Chlorella vulgaris. *Planta* **143:** 225–231.
Starzecki, W. (1961): An improved microrespirometer and extension of its application over plants with big leaves. *Acta Soc. Bot. Pol.* **30:** 327–343.
West, P. W., Gaeke, C. C. (1956): Fixation of sulfur dioxide as disulfitomercurate and subsequent estimation. *Anal. Chem.* **12:** 1816–1819.
Wong, C. H., Klein, H., Jäger, H. J. (1977): The effect of SO_2 on the ultrastructure of Pisum and Zea chloroplasts. *Angew. Bot.* **51:** 311–319.
Ziegler, I. (1972): The effect of SO_3^- on the activity of ribulose-1,5-diphosphate carboxylase in isolated spinach chloroplasts. *Planta* **103:** 155–163.
Ziegler, I. (1973): Effect of sulphite on phosphoenolopyruvate carboxylase and malate formation in extracts of Zea mays. *Phytochem.* **12:** 1027–1030.
Zurzycki, J. (1955): A micromethod for measuring photosynthesis. *Experientia* **11:** 261–262.
Zurzycki, J. (1970): Some improvements of the microrespirometric technique. *Acta Soc. Bot. Pol.* **39:** 497–507.

Acta Botanica Hungarica 33 (1–2), pp. 59–61 (1987)

ADAPTIVE RESPONSES OF WOODY INTRODUCENTS IN THE BOTANICAL GARDENS OF YEREVAN (SOVIET UNION) AND VÁCRÁTÓT (HUNGARY)

V. V. Kazaryan

BOTANICAL INSTITUTE OF ARMENIA, YEREVAN, SOVIET UNION

(Received: 15 October 1985)

The author studied the different forms of carbohydrates and nitrogen, and the mineral content in freshly fallen leaves of woody introducents developing under the conditions of the Yerevan and Vácrátót botanical gardens. As it has turned out, the more the leaves become clear of assimilates before defoliation, the better the plant has adapted itself to the conditions of the site.

Introduction

Replenishment of storage tissues with energy carriers: carbohydrates (Tumanov 1931, Vassilyev 1958, Sergeyeva 1971), proteins (Sergeyeva and Polyakova 1964, Kandarova 1964, Duseyeva 1974), lipids (Romanovskaya 1960, Gulisashvili et al. 1979), macroerg compounds (Sergeyeva 1971), is considered to be one of the important adaptive responses of woody plants to the difficult winter conditions of living. Plants richer in trophic materials show incomparably higher winterhardiness.

The active transport of assimilates from the leaves to the storage tissues begins with a decrease in the rate of growth, which takes place in the summer months, a period favourable for the life processes of plants, and which is determined first of all by a change in the length of days (Potapenko 1971). When the growth is completed all photosynthetic products of the leaves flow towards the storage tissues. This process takes place during the period of defoliation in autumn, when the fermentative decomposition of structural elements in the living cell becomes more intensive, mobile trophic compounds are formed which also are carried to the storage tissues and improve the general energetic balance of the plant. In this contect it was found that those woody plants whose leaves become relatively clearer in the autumn period show a better winterhardiness (Voronova 1972, Kazaryan 1979).

The plants chosen in the course of previous investigations as subjects of examination differed, though, in range of distribution, still were placed under uniform conditions in the Yerevan Botanical Garden. In order to obtain important and more characteristic results it became necessary to raise these plants under totally different geographical and ecological conditions. To this end — owing to the joint work of those employed in the botanical gardens of Yerevan and Vácrátót — adequate introduction plots were established at both experimental sites.

Materials and methods

The experiment included three plant groups differing in geographic distribution. The distribution area for the plants of group I [*Populus bolleana* Lauche, *Brussonetia papyrifera* (L.) L'Herit, *Catalpa ovata* G. Don, *Chaenomeles japonica* (Thumb.) Lindl.] is South-East and Central Asia.

Group II was formed by species distributed over the European parts of the Soviet Union and in Central Europe (*Quercus robur* L., *Ulmus laevis* Pall., *Lonicera tatarica* L., *Acer tataricum* L.).

The species of group III (*Quercus macranthera* Fisch. et Mey., *Tilia caucasica* Rupr., *Lonicera caucasica* Pall., *Betula litwinowii* A. Doluch., *Populus gracilis* Grossh.) live in the Caucasus.

Freshly fallen yellow autumn leaves were studied and the carbohydrate content in them determined by JENSEN HAGGEDORN's method, while the quantities of various forms of nitrogen were obtained by the KJELDAHL technique (BELOZERSKY and PROSKURIKOV 1951); the ash left behind was also analysed.

Results and discussion

Soluble carbohydrates were contained in larger quantities in the leaves of plants at Vácrátót, in all three groups of plants, as shown by the diagram (Fig. 1). In this context it deserves mentioning that under the conditions of Vácrátót the minimum of sugar content was found with plants originating from the European parts of the Soviet Union, whose living conditions more or less agree with those at Vácrátót. On the contrary, the leaves of the Caucasian plants turned yellow and fell with lower sugar contents under the conditions of Yerevan. Under the conditions of Vácrátót the fallen leaves contained about twice as much or even more soluble carbohydrates. The fallen leaves of the representatives of vegetation in South-East and Central Asia were rich in sugar both in Yerevan and at Vácrátót.

Analyses for starch content gave a different picture. Under the conditions of Yerevan — compared to Vácrátót — the leaves of plants in all three groups contained larger quantities of starch. In the present case the temperature conditions under which defoliation occurred supposedly played an important role. Under the ecological conditions of Yerevan this process is determined first of all by a rapid fall in the air temperature. According to the data of BYUSGEN (1961) the low temperature does not allow the starch time to decompose, so it is left behind in the yellow leaves; that is, the cold inhibits the hydrolytic decomposition. The defoliation of woody plants in Central

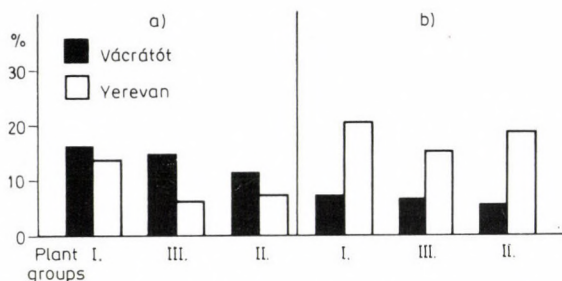



Fig. 1. Soluble carbohydrate (a) and starch (b) content in fallen leaves of woody introducents (% of drymatter)

Europe is — in accord with the gradual cooling of air — a more even process, which promotes the fermentative decomposition of starch, and the transportation of sugar to the storage organs.

As for the total and protein nitrogen contents the following facts were established (Fig. 2). In all three groups of plants at Vácrátót the total and protein nitrogen contents of leaves at the time of defoliation were lower than

mg %
3.0
2.0
1.0
0
a)
b)
Vácrátót
Yerevan
Plant groups I. III. II. I. III. II.

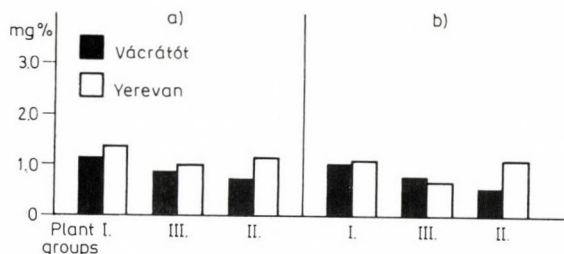



Fig. 2. Total (a) and protein nitrogen (b) content in fallen leaves of woody introducents (% of drymatter)

%
15
10
5
0
Vácrátót
Yerevan
Plant groups I. III. II.

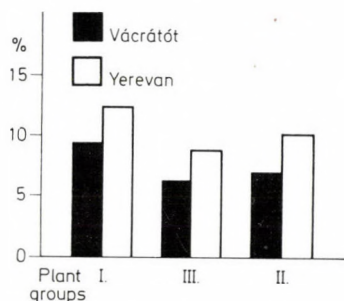



Fig. 3. Mineral content in fallen leaves of woody introducents (% of drymatter)

in Yerevan. At the same time, the minimum total and protein nitrogen content of leaves was found for the plants of group II under the conditions of Vácrátót, and for the representatives of the Caucasian vegetation in the Yerevan Botanical Garden.

In the course of analysing the mineral content (Fig. 3) it became clear that — similarly to the result of the nitrogen content analysis — there was more of minerals in the fallen leaves of introducents in the Yerevan Botanical Garden than in the case of plants developing under the conditions of Vácrátót. Further, under the conditions of Yerevan a relatively lower mineral content of fallen leaves was pointed out for the representatives of the Caucasian dendroflora. Under the ecological conditions of Vácrátót the amount of ash components in the leaves of plants originating from the European parts of the Soviet Union was lower only in comparison to the Caucasian species.

Thus, as seen from the data obtained, the minimum value of assimilate content in fallen leaves was pointed out in the Vácrátót Botanical Garden for the plants from the European part of the Soviet Union, while under Yerevan conditions for the plant representatives of the Caucasus. All this suggests that the assimilate content of fallen leaves may be indicative of the plants' adaptation to the new life conditions. Consequently, as it was pointed out earlier (Kazaryan 1979), the more the plant has become adapted to the site conditions, the better its leaves get rid of the assimilates before defoliation.

REFERENCES

Belozersky, A. N., Proskurikov (1951): *Practical Guide to Plant Biochemistry*. Moscow, Sovietskaya Nauka, pp. 388.

Byusgen, M. (1961): *Structure and Life of Forest Trees*. Goslesbumizdat, Moscow, pp. 424.

Duseyeva, F. A. (1974): Annual dynamics of phosphorus compounds in certain species forming forest stands. In: *Physiology and Biochemistry of Winterhardiness in Woody Plants*. UFA, 61–75.

Gulisashvili, V. Z., Kandelaki, A. A., Kapanadze, J. J. (1979): *Transformation of Nutrient Reserves in Woody Plants in Connection with Winterhardiness*. Mecniereba, Tbilisi. pp. 70.

Kazaryan, V. V. (1979): Water and plastic matter content in fallen leaves of woody introducents. *Bulletin GPSZ*, **3:** 79–82.

Kandarova, I. B. (1964): Peculiarities of nitrogen metabolism in frost resistant and frost sensitive plants. In: *Physiology of Winterhardiness in Woody Plants*. Nauka, Moscow. 61–73.

Potapenko, A. I. (1971): *Bioregulation of Plant Development*. Rostov, pp. 327.

Romanovskaya, O. I. (1960): Physiological–biochemical characteristics of cherry hybrids of different winterhardiness. In: *Physiology of Winterhardiness in Plants*. Akad. Nauk, Moscow. 288–290.

Sergeyeva, K. A. (1971): *Physiological and Biochemical Grounds of Winterhardiness in Woody Plants*. Nauka, Moscow. pp. 174.

Sergeyeva, K. A., Polyakova, P. B. (1964): Changes of nucleic acids in woody plants as related to winterhardiness. In: *Physiology of Winterhardiness in Woody Plants*. Nauka, Moscow. 53–60.

Tumanov, I. I. (1931): *Winterhardiness of Plants*. Szelkhozgiz, Moscow–Leningrad. pp. 120.

Vassilyev, I. M. (1958): *Hibernation of Plants*. Akad. Nauk. SSSR, Moscow. pp. 308.

Voronova, N. V. (1972): Az almafák leveleinek cukor- és nitrogéntartalma ősszel, a télállósággal összefüggésben. In: A növények adaptációjának és állóképességének fiziológiai mechanizmusai (Sugar and nitrogen contents in leaves of apple-trees in autumn, as related to winterhardiness. In: *Physiological Mechanisms of Adaptation and Endurance in Plants*). Nauka. Moscow. 204–207.

Acta Botanica Hungarica 33 (1–2), pp. 63–66 (1987)

CHLORIDIUM CARPATICUM, A NEW SPECIES WITH BROWN PIGMENTED CONIDIA

VĚRA HOLUBOVÁ-JECHOVÁ* and ÁGNES RÉVAY**

* BOTANICAL INSTITUTE, CZECHOSLOVAK ACADEMY OF SCIENCES, 252 43 PRŮHONICE NEAR PRAHA, CZECHOSLOVAKIA
** HUNGARIAN NATURAL HISTORY MUSEUM, BOTANICAL DEPARTMENT, BUDAPEST, KÖNYVES K. KRT. 40. H-1476, HUNGARY

(Received: 1 August 1986)

A new species of *Chloridium* Link, *Chloridium carpaticum* Hol.-Jech. et Révay, is described and illustrated from dead wood collected in Central Europe — Hungary and Czechoslovakia. *Ch. carpaticum* belongs to sect. *Gongromeriza* (Preuss) W. Gams et Hol.-Jech.; its relationship to other species is briefly discussed.

Chloridium carpaticum Hol.-Jech. et Révay spec. nova

Coloniae effusae, brunneae, pilosae. Mycelium plerumque in substrato immersum, ex hyphis ramosis, septatis, subhyalinis vel pallide brunneis, laevibus, 1,5–2,5 μm crassis compositum. Conidiophora solitaria, erecta, simplicia, recta vel leniter flexuosa, septata, brunnea, ad basin atrobrunnea, apicem versus pallidiora, laevia, 100–250 μm long, 4–6 μm crassa, ad basin 7–10 μm inflata, ad apicem angustata, usque 3 μm crassa; colla infundibuliformia vel cupulata vel interdum cylindrica et leniter dilatata, usque ad 7 μm lata et 5 μm longa. Conidiophora saepe percurrenter prolificantia. Conidia in capitulis mucidis aggregata, oblongo-ellipsoidea, allantoidea, pallide brunnea vel brunnea, (9,5–)10–14 × 3,5–5,5 μm (plerumque 11–12 × 4–4,5 μm), in finibus ambis vel in fine uno cum poro germinali praedita.

Habitat in ligno et cortice putrido *Fagi sylvaticae*. Holotypus: Hungaria, montes Bükk-hegység, in valle "Rejteki-völgy" prope pag. Répáshuta; ad ramum putr. *Fagi sylvaticae*; 10. X. 1984, leg. Á. RÉVAY (BP 656 Fn.).

Colonies effuse, brown, hairy. Mycelium mostly immersed in the substrate, composed of branched, septate, subhyaline to pale brown, smooth, 1.5–2.5 μm wide hyphae. Conidiophores solitary, erect, unbranched, straight or slightly flexuous, septate, brown, dark brown at the base, paler towards the apex, smooth, 100–240 μm long, 4–6 μm wide, swollen up to 7–10 μm at the base, narrowing up to 3 μm wide in the upper part below the collarette. Collarette funnel-shaped or cup-shaped up to flaring or sometimes only cylindrical and slightly widening, up to 7 μm in diameter and 5 μm deep. Percurrent proliferation frequently several times repeating, giving to the conidiophore a geniculate appearance. Conidia produced singly, successively, within the collarette, aggregated in slimy masses, oblong-ellipsoidal, allantoid or occasionally straight, continuous, pale brown to brown, (9.5–)10–14 × 3.5–5.5 μm, mostly 11–12 × 4–4.5 μm, usually at one or both ends with a thinner and paler germ pore.

On dead wood and bark of *Fagus silvatica*.

Additional material studied:

Hungaria: montes Bükk-hegység, in valle "Rejteki-völgy" prope pag. Répáshuta; ad ramum putr. *Fagi sylvaticae*; 30. V. 1985, leg. Á. RÉVAY et J. GÖNCZÖL.

Bohemoslovacia: Moravia, montes Moravskoslezské Beskydy, in declivi septentr. montis V. Polana, in silva virginea Mionší dicta, apud pagum Horní Lomná, haud procul ab oppido Jablunkov; ad corticem putr. *Fagi sylvaticae*, 28. VII. 1982, leg. V. HOLUBOVÁ-JECHOVÁ (PRM 842724).

Conidium ontogeny in *Chloridium* Link is recognized as a principal criterion in the infra classification of the genus. In a detailed study W. GAMS and HOLUBOVÁ-JECHOVÁ (1976) accepted three sections in *Chloridium*: sect. *Chloridium* characterized by phialides with multiple conidiogenous loci active within the collarette, sect. *Gongromeriza* (Preuss) W. Gams at Hol.-Jech. characterized by phialides with a single basipetal sequence of conidia formed within a collarette and sect. *Psilobotrys* (Sacc.) W. Gams et Hol.-Jech. where the phialides are constricted at the tip to a narrow collarette and mostly proliferate sympodially. *Chloridium carpaticum* belongs to the section *Gongromeriza* characterized by conidiophores in which serial production of conidia takes place from a single conidiogenous locus within the pronounced collarette. Equally as at all species of this section — successive conidium formation at this new species — leads to the formation of slimy heads. After production of a series of conidia, percurrent proliferation commonly occurs. The process of sporulation and proliferation is obviously repeated several times, leading to distinctive geniculate conidiophores.

Ch. carpaticum occupies an extraordinary position in the section *Gongromeriza* and in the genus, too, by its large, brown pigmented conidia. Also its conidia are slightly thick walled and have a paler and thinner small germ pore at both or only at one end of conidia. Nearly all species of *Chloridium* have hyaline conidia. Only sect. *Gongromeriza* includes some species with brown pigmented conidia, e.g. *Ch. phaeosporum* W. Gams et Hol.-Jech. characterized by its shorter conidiophores and smaller conidia (conidia $4–5 \times 1.7–2.2$ μm). *Ch. pachytrachelum* W. Gams et Hol.-Jech., a further member of the section with quite large conidia ($5–7.5 \times 2.5–3.5$ μm), has hyaline conidia which mature and dry are brownish in mass. *Ch. carpaticum* by the shape and size of its conidia and conidiophores is close to *Ch. lignicola* (Mangenot) W. Gams et Hol.-Jech., which conidia are oblong-ellipsoidal, sometimes slightly allantoid, hyaline, $3.5–5(–7) \times 1.5–2$ μm. *Ch. carpaticum* has, however, conidia distinctly brown pigmented, slightly thick-walled and larger, $10–14 \times 3.5–5.5$ μm. Similar as at *Ch. lignicola* it is possible to observe also more than one conidium remaining the collarette. *Ch. carpaticum* is close also to *Ch. matsushimae* W. Gams et Hol.-Jech. mostly by the repeating of percurrent proliferation forming geniculate conidiophores and by large conidia, which at *Ch. matsushimae* are $15–19 \times 3.6–5.3$ μm, hyaline and brownish when dry, with a slimy apical appendage. *Ch. carpaticum* occasionally forms its conidia also beyond the collarette on a small protruding meristem, and presents therefore a link to the section *Chloridium* with multiple conidiogenous loci. Similar mode of conidio-

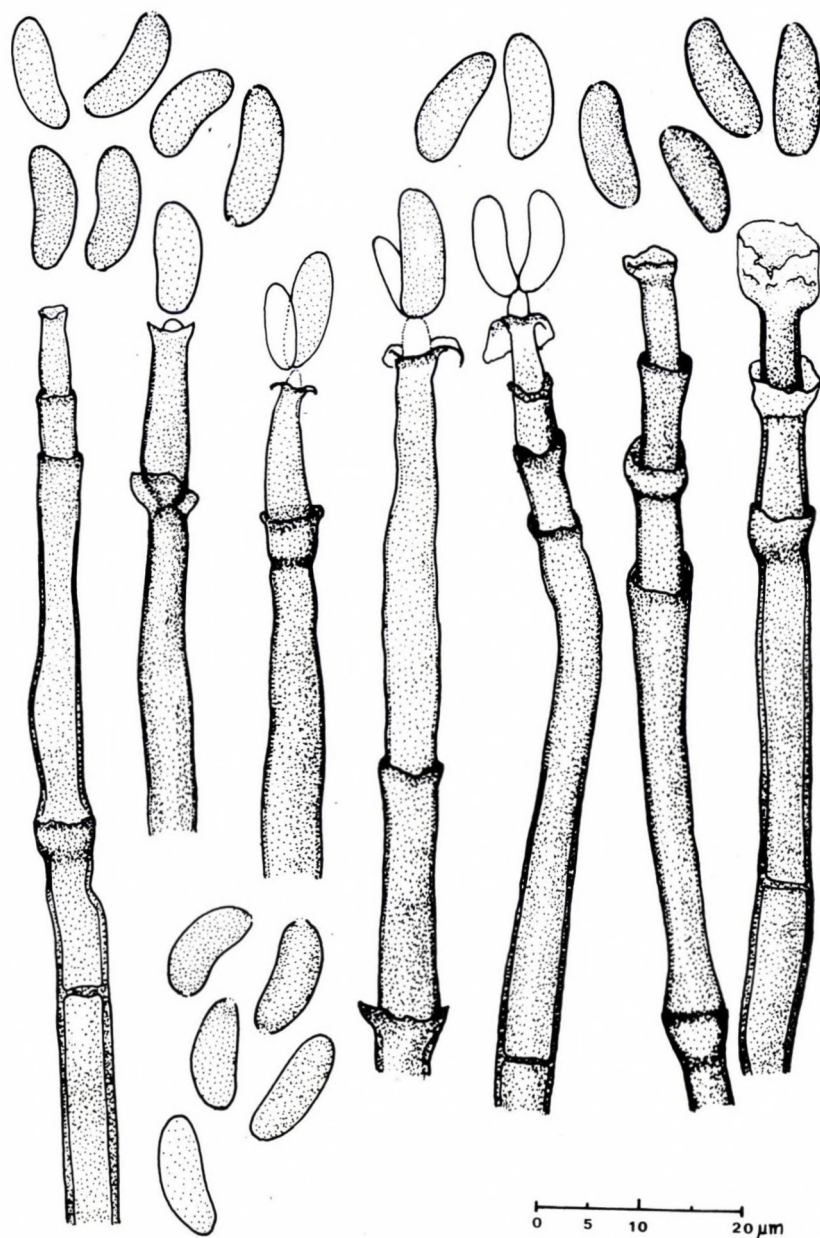



Fig. 1. Chloridium carpaticum Hol.-Jech. et Révay — conidiophores and conidia. Del. V. Holubová-Jechová

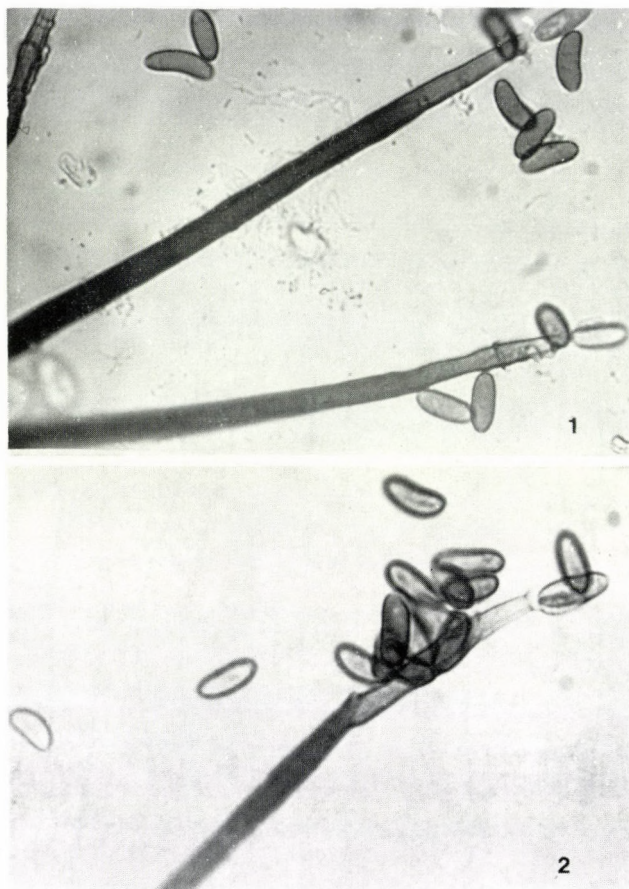



Plate I
1–2. Chloridium carpaticum — conidiophores and conidia, ×1000

genesis is present in *Cacumisporium capitulatum* (Corda) Hughes, which conidia are elongate ellipsoidal, allantoid, brown pigmented in age, 3-septate, 15–22× 5–6.5 μm. It seems that *Ch. carpaticum* occupies an intermediate position between *Chloridium* and *Cacumisporium*, but as the phialide opening is much wider and deeper than in *Cacumisporium*, and its conidia are aseptate and conidiophores distinctly percurrently proliferate, it is classified in *Chloridium* here.

REFERENCES

Gams, W., Holubová-Jechová, V. (1976): *Chloridium* and some other dematiaceous Hyphomycetes growing on decaying wood. *Studies Mycol., Baarn* **13:** 1–99.

Acta Botanica Hungarica 33 (1–2), pp. 67–73 (1987)

NEW OR INTERESTING HYPHOMYCETES ON FOREST LITTER FROM HUNGARY

ÁGNES RÉVAY

HUNGARIAN NATURAL HISTORY MUSEUM, BOTANICAL DEPARTMENT,
BUDAPEST, KÖNYVES K. KRT. 40. H-1476, HUNGARY

(Received: 1 May 1986)

Four dematiaceous hyphomycetes are reported from Hungary. *Endophragmiella bükkensis* sp. nov. and *Triadelphia hungarica* sp. nov. are described, *Triadelphia uniseptata* is reported from Hungary for the first time and additional information is recorded for *Triadelphia heterospora*.

During a survey of forest litter Hyphomycetes in Hungary some interesting or noteworthy species were found. The collected material derived from aquatic habitats: mountain streams and from the water of tree-hollows. The tree-hollows proved to be an interesting biotop not only for aquatic and aero-aquatic, but for dematiaceous hyphomycetes, too. (GÖNCZÖL 1976, GÖNCZÖL and RÉVAY 1983, RÉVAY 1985 in press.)

Three species of *Triadelphia* collected from tree-hollows on several forest debris, and a new species of *Endophragmiella* collected on spruce-cone from the water of a mountain stream are reported in this paper.

Endophragmiella bükkensis Révay sp. nov. (Plate I/1–2)

Coloniae effusae, pilosae, atrobrunneae. Mycelium partim superficiale sed in substrato plerumque immersum, ex hyphis pallide brunneis usque brunneis, laevibus, septatis, 1,5–3 μm latis compositum. Conidiophora macronemata, mononemata, solitaria, erecta, simplicia, recta vel leniter flexuosa, subcylindrica, laevia, brunnea, ad apicem pallidiora, 30–40 μm longa per proliferationes successivas percurrentes conidiogenas usque ad 110 μm longa, 3,2–3,5 μm lata, ad basim 4–5,5 μm. Cellulae conidiogenae terminales, percurrentes, monoblasticae. Conidia acrogena, solitaria, pyriformia vel ellipsoidea, ad septa interdum leviter constricta, laevia, pallide brunnea, 1–(2–)-septata, 20–28 × 5–8,5 μm, ob partem fractam cellulae conidiogenae fimbriata. Cellula superior conidii parum longior vel aequalis inferiori.

Holotypus: Hungaria, montes Bükk-hegység ad rivum Pénz-patak pr. pag. Répáshuta; ad storbilum putr. deiect. *Piceae abietis*, 30. V. 1985, leg. Á. RÉVAY et J. GÖNCZÖL (BP 657 Fn.).

Colonies effuse, hairy, dark brown. Mycelium partly superficial but mostly immersed in the substratum, composed of pale brown to brown, smooth, septate hyphae, 1.5–3 μm wide. Conidiophores macronematous, mononematous, solitary, erect, simple, straight or slightly flexuous, subcylindrical, septate at 10–19 μm intervals, smooth, brown, paler towards the apex, at first 30–40 μm long, 3.2–3.5 μm wide, 4–5.5 μm wide at the base. Proliferated conidiophores reach a length of 110 μm. Conidiogenous cells integrated, terminal, percurrent,

monoblastic. Conidiogenous cell forming on each successive percurrent proliferation of the penultimate cell through the conidiogenous cell and beyond the open end that formed as a result of rhexolytic conidium secession. Conidia acrogenous, solitary, pyriform or ellipsoidal, slightly constricted at the septa, septum partly obscured by a dark band of wall, smooth, pale brown to brown, 1-septate (rarely 2-septate), 20–28 × 5–8.5 μm, with a small basal frill from the apex of the conidiogenous cell. The upper cell is slightly longer or the same size as the lower cell is. Specimen examined: On spruce-cone of *Picea abies* (L.) Karsten; Hungary, Mts. Bükk-hegység, from the stream Pénz-patak near Répáshuta, 30. V. 1985, Á. Révay and J. Gönczöl (BP 657 Fn.), holotype.

In a detailed study Hughes (1979) recognized 33 species of the genus *Endophragmiella*. Subsequently 13 additional species have been described by Kirk and Dunn. Kirk (1985) has produced a key to the 46 described species of *Endophragmiella*. *Endophragmiella bükkensis* differs from all the species included by Kirk. The conidia of *E. bükkensis* are superficially similar to those of: *E. boewei* (Crane) Hughes and *E. pinicola* (Ellis) Hughes. However *E. bükkensis* is distinguished from *E. boewei* by its distinctly narrower conidia, and from *E. pinicola* by its longer conidia. *Endophragmiella bükkensis* by the shape of its conidia is close to *E. resinae* P. M. Kirk, which conidia are obovoid to pyriform, 1-septate, 17–22 × 9–10.5 μm, with a distinct basal frill. However the conidia of *E. bükkensis* are longer and slightly narrower with an inconspicuous basal frill.

Triadelphia hungarica Révay sp. nov. (Plate I/3–4, II/1–4)

Mycelium in substrato immersum, ex hyphis ramosis, septatis subhyalinis usque pallide brunneis, laevibus, 1,8–2,5 μm crassis compositum. Cellulae conidiogenae e mycelio ortae gregariae usque caespitosae, cylindricae, ampulliformes vel globosae, hyalinae usque pallide brunneae, holoblasticae, monoblasticae, determinatae, 5–9 × 3,5–4,5 μm. Conidia acrogena, solitaria, blastica; ad substrata naturalia duae formae conidiorum adsunt: (a) conidia clavata vel paene cylindrica, apicibus ambobus rotundata, 17,6–20,8 × 6,4–7,0 μm, in statu juvenili hyalina, mature atrobrunnea, cellula basali subhyalina, laevia, 2-septata, septo apicali taenia nigra 2,5–3,2 μm lata tecto; (b) conidia fusiformia-ellipsoidea, recta vel parum inclinata, 6–7-septata, in medio taenia nigra 2,5–3,5 μm lata, cellulis apicalibus et basalibus hyalinis vel subhyalinis, cellulis centralibus pallide brunneis usque atrobrunneis, basi truncata, 32–36 × 8–10 μm, apice nonnunquam appendicem longam hyalinam gerentia.

Holotypus: Hungaria, Comitatus Zala, pr. pag. Bak; ad detritum ex caverna arboris (*Quercus* sp.), 22. VIII. 1985, leg.: J. Gönczöl (BP 658 Fn.).

Mycelium mostly immersed in the substrate, composed of branched, septate, subhyaline to pale brown, smooth, 1.8–2.5 μm wide hyphae. Conidiogenous cells gregarious to caespitose, arising from undifferentiated hyphae, cylindrical or ampulliform to globose, hyaline or pale brown, holoblastic, monoblastic, determinate, 5–9 × 3.5–4.5 μm. Conidia acrogenous, solitary, blastic, two morphologically different forms were found on natural substrate:

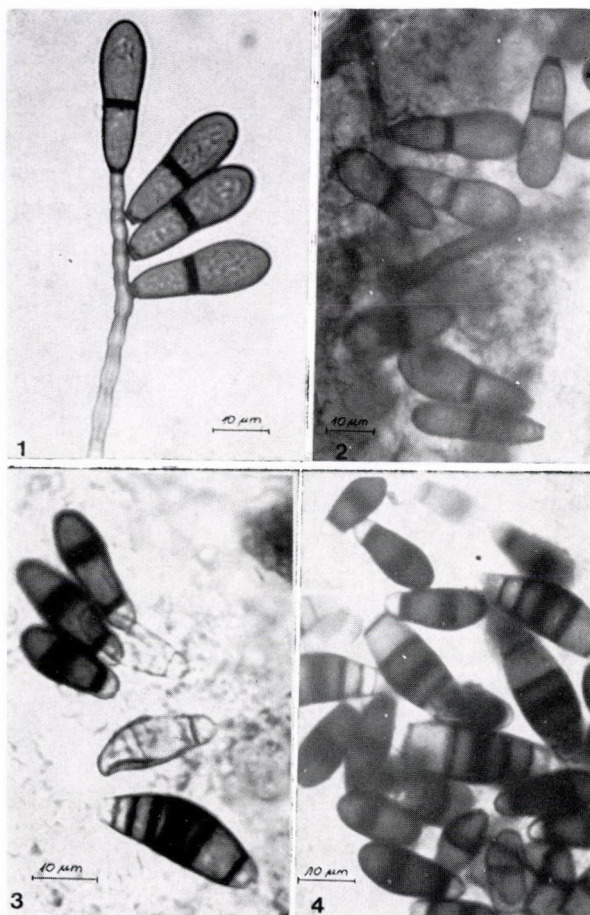



Plate I

1. Endophragmiella bükkensis — conidiophore with conidia
2. Detached conidia of *Endophragmiella bükkensis*
3–4. Two conidia forms of *Triadelphia hungarica*

(a) Conidia clavate or slightly cylindrical, tip and base rounded, 17.6–20.8 × 6.4–7 μm, hyaline when young, becoming dark brown when mature, the basal cell subhyaline, smooth, 2-septate, the apical septum covered by a black 2.5–3.2 μm wide band.

(b) Conidia fusiform-ellipsoidal, straight or slightly curved, 6–7-septate, with a dark 2.5–3.5 μm wide band in the middle, end cells hyaline to subhyaline, central cells pale brown to dark brown, truncate at the base, 32–36 × 8–10 μm, sometimes with a long hyaline appendage on the apical cell.

Specimen examined: On debris from a tree-hollow (*Quercus* sp.); Zala County, near the village Bak, 22. VIII. 1985, J. Gönczöl (BP 658 Fn.), holotype.

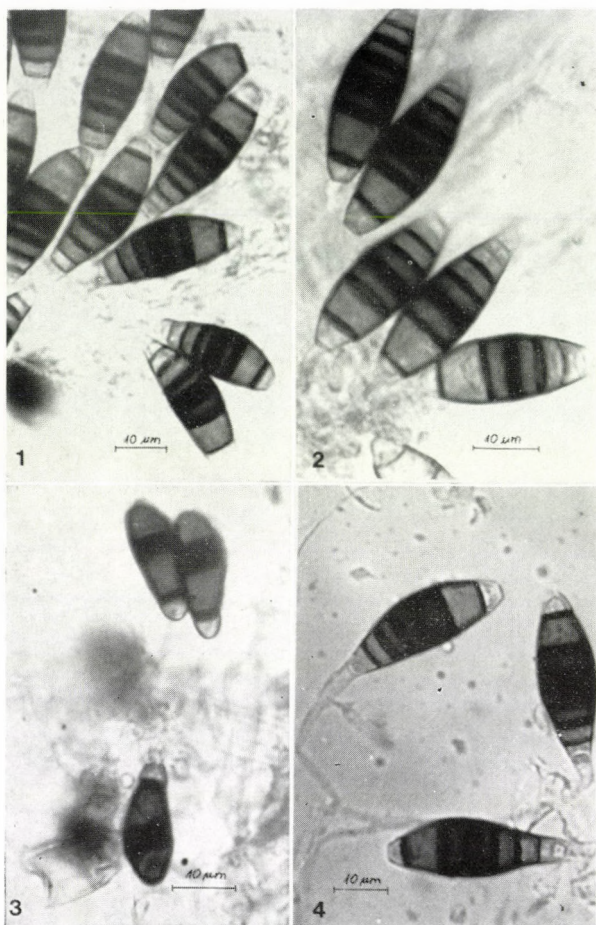



Plate II

1., 2., 4. The (b) conidia form of *Triadelphia hungarica* — 2. conidia on conidiogenous cells; 4. three conidia with long hyaline appendage
3. The (a) conidia form of *Triadelphia hungarica*

Triadelphia heterospora Shearer et Crane, Mycologia 63: 247 (1971). (Plate III/1–2)

Conidiogenous cells subspherical, 3–5 × 2.5–3.5 μm, formed a sporodochium-like structure on natural substrate. Conidia of two different forms were found:

(a) Cylindrical, pale brown, 2-septate, the apical septum wider than the other one, rounded at the apex, slightly truncated at the base, 16–20 × 3.5–5.0 μm.

(b) Cylindrical-fusiform, pale brown, basal cell subhyaline, 4–(5)-septate, 24–27.5 × 6–7 μm.

Specimen examined: On debris from a tree-hollow; Zala County, near the village Bak, 22. VIII. 1985, J. GÖNCZÖL.

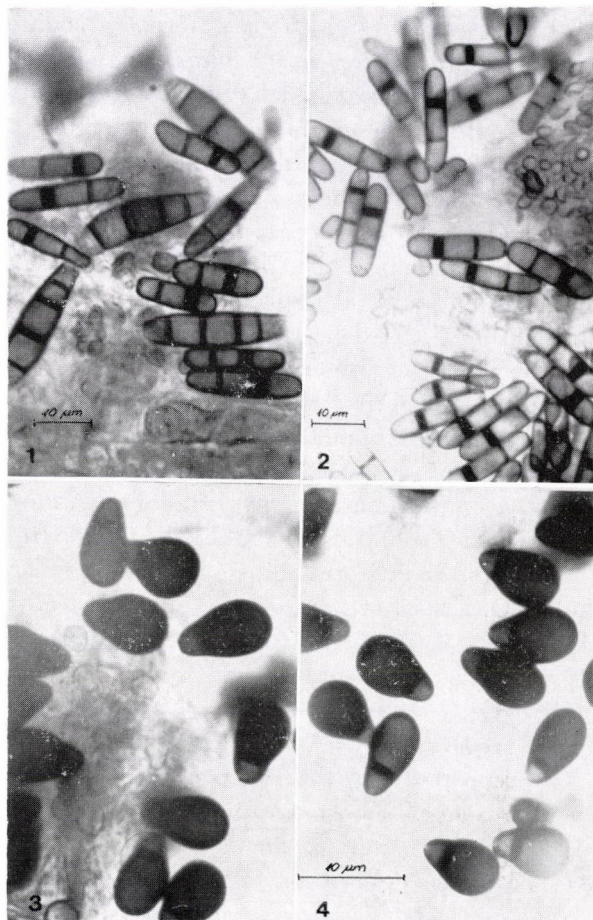



Plate III

1–2. Conidia of *Triadelphia heterospora*
3–4. Conidia of *Triadelphia uniseptata*

Triadelphia uniseptata (Berk. et Br.) P. M. Kirk, Trans. Br. Mycol. Soc. 80 (3): 464 (1983). (Plate III/3–4)

Colonies effuse, blackish brown. Conidiogenous cells ampulliform to globose, monoblastic, determinate, 4–8.5 × 3–4.5 μm. Conidia acrogenous, solitary, obovoid to broadly obovoid, 1-septate, brown to dark brown, 11.5–16 × 6.4–9 μm.

Specimen examined: On debris from a tree-hollow; Zala County, near the village Bak, 22. VIII. 1985, J. Gönczöl.

The genus *Triadelphia* Shearer et Crane (1971) was established for a single species *Triadelphia heterospora*, isolated from submerged balsawood,

characterized by the presence of two different forms of conidia. In a revision of the genus *Dicoccum* Corda *Dicoccum inquinans* Sacc. was transferred to *Triadelphia* by HUGHES and PIROZYNSKI (1972). Two additional species *T. loudetiae* and *T. pulvinata* was described by MAGGI et al. (1978) from soil. CONSTANTINESCU and SAMSON (1982) discussed the four known species of *Triadelphia* and described *T. romanica* as a new species from a hen egg shell, as well as a new combination *T. alabamensis* was proposed by them in a detailed study. The examinations of the species of *Triadelphia* showed that the genus is extremely pleomorphic, each species producing two to five different forms of conidia. The only exception is the *Triadelphia uniseptata*, which has only one conidium form. This new combination was proposed by KIRK (1983).

The new species described here has two morphologically distinct conidia and both conidia form showed abundant sporulation. The (a) conidia resemble to the "type a" conidia of *T. heterospora*, although the latter are always cylindrical, pale brown and thinner. The (a) conidia of *T. hungarica* generally clavate, dark brown and the basal cell subhyaline. The (b) conidia of the new species are similar to the fusiform-ellipsoidal conidia of *Triadelphia alabamensis* (Matsushima) O. Const. et Samson (basionym: *Stemphyliomma alabamensis* Matsushima, Mat. Mycol. Mem. **2:** 12, 1981), but they are longer and wider (28–44 $\times$ 10.5–16 μm, 6–8-septate) and do not become curved when mature.

Triadelphia heterospora has been found in Hungary for three occasions by TÓTH (1975). He reported only the cylindrical, 2-septate conidia. In the course of a reexamination of the herbarium material (on *Sambucus nigra*) collected by him, I have seen some of the "type b" conidia form, too. They agreed in every respect of the description of "type b" conidia of the holotype. In the present collection reported here abundant sporulation of "type a" conidia was found, but the "type b" conidia were somewhat different from the holotype.

ACKNOWLEDGEMENTS

The author is grateful to Professor S. J. HUGHES (Biosystematic Research Institute, Ottawa, Canada) for his suggestion in the taxonomic work and to Dr. S. TÓTH (University of Agricultural Sciences of Gödöllő, Hungary) for help with the Latin diagnosis.

REFERENCES

Constantinescu, O., Samson, R. A. (1982): *Triadelphia*, a pleomorphic genus of Hyphomycetes. *Mycotaxon* **15:** 472–486.

Gönczöl, J. (1976): Ecological observations on the Aquatic Hyphomycetes of Hungary, II. *Acta Bot. Hung.* **22:** 51–60.

Gönczöl, J., Révay, Á. (1983): Observations on the Hyphomycetes inhabiting forest litter of Hungary. *Acta Bot. Hung.* **29:** 107–125.

Hughes, S. J., Pirozynski, K. A. (1972): *Dicoccum* Corda. *Canad. J. Bot.* **50:** 2521–2534.

Hughes, S. J. (1979): Relocation of species of *Endophragmiella* auct. with notes on relevant generic names. *New Zealand J. Bot.* **17:** 139–188.
Kirk, P. M. (1983): New or interesting microfungi IX. Dematiaceous Hyphomycetes from Esher Common. *Trans. Br. mycol. Soc.* **80** (3): 449–467.
Kirk, P. M. (1985): New or interesting microfungi XIV. Dematiaceous Hyphomycetes from Mt. Kenya. *Mycotaxon* **23:** 305–352.
Maggi, O., Bartoli, A., Rambelli, A. (1978): Two new species of *Triadelphia* from rhizosphere of *Loudetia simplex* in the Ivory Coast. *Trans. Br. mycol. Soc.* **71:** 148–154.
Matsushima, T. (1981): Matsushima Mycological Memoirs No. 2. *Matsushima Fungus Coll.*, Kobe.
Shearer, C. A., Crane, J. L. (1971): Fungi of the Chesapeake Bay and its tributaries. I. Patuxent River. *Mycologia* **63:** 237–260.
Tóth, S. (1975): Rare microscopic fungi from Hungary. *Bot. Közlem.* **62:** 13–18.

Acta Botanica Hungarica 33 (1–2), pp. 75–79 (1987)

HIFOMICETES DE TOPES DE COLLANTES, CUBA
II. ESPECIES ENTEROBLÁSTICAS

JULIO MENA PORTALES y ANGEL MERCADO SIERRA

INSTITUTO DE BOTÁNICA, ACADEMIA DE CIENCIAS DE CUBA, LA HABANA, CUBA

(Llegado: 15 Marzo 1986)

Fourteen species of saprophytic and enteroblastic hyphomycetes belonging to nine genera from Topes de Collantes, Sancti Spiritus province, Cuba are recorded. One genus and five species are new records from Cuba and *Chloridium obclaviforme* is described as new species.

Introduccion

Este artículo constituye la segunda parte del estudio taxonómico de los hifomicetes de Topes de Collantes, una de las elevaciones más prominentes de la Sierra del Escambray en la provincia de Sancti Spíritus, Cuba. En un primer trabajo se incluyeron las especies con conidiogénesis holoblástica, mientras que en éste, se agrupan las especies que presentan conidiogénesis enteroblástica.

Aquí relacionamos 14 especies de hifomicetes distribuídas en 9 géneros, de los cuales un género y 5 especies constituyen nuevos reportes para Cuba, incluida una especie del género *Chloridium* Link ex Fr. que se propone como un nuevo taxon para la ciencia. Los ejemplares y tipos correspondientes se encuentran depositados en el Herbario del Instituto de Botánica de la Academia de Ciencias de Cuba (HAC).

Reseña de especies

Chloridium claviforme (Preuss) W. Gams et Hol.-Jech., Studies in Mycology., 13: 31–33 (1976)*

Sobre ramas muertas de *Smilax* sp. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7035 (HAC).

Colonias dispersas, pardo oliváceas a pardo oscuras, pelosas. Conidióforos erectos, rectos o flexuosos, pardo algo oscuros a pardo oscuros, ligeramente más pálidos hacia el ápice, lisos; 18–30 μm de longitud si consisten en una simple fiálide, normalmente de 45–100 μm de longitud por 3–4,5 μm de grosor. Fiálides con collarín acampanado o en forma de vaso o embudo. Fialoconidios en cabezas mucilaginosas, pequeños, sin septor, subhialinos, cuneiformes o claviformes, con la base truncada o atenuada, lisos; 2,5–3 × 1,5–2,5 μm.

Esta especie es muy común en Europa y América del Norte. El reporte para Cuba es, posiblemente, el primero para un pais tropical.

Chloridium lignicola (Mangenot) W. Gams et Hol.-Jech., Studies in Mycology., 13: 37 (1976)**

* Especie nueva para Cuba
** Género y especie nuevos para Cuba

Sobre corteza de tronco muerto no identificado. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7033 (HAC).

Colonias dispersas, pardo oliváceas a pardo oscuras, pelosas. Conidióforos erectos, rectos o flexuosos, pardo oliváceos, más pálidos hacia el ápice, lisos; 70–165 μm de longitud por 2,5–3,5 μm de frosor. Fiálides muy constreñidas hacia el extremo apical, expandiéndose después en un collarín acampanado. Fialoconidios en cabezas mucilaginosas, pequeños, sin septos, hialinos a subhialinos, oblongo-elipsoidales o alantoides, lisos; 3,5–5 × 1,5–2(–2,5) μm.

Esta especie se ilustra en este trabajo por constituir un nuevo reporte para Cuba y por tener la distribución mundial limitada a algunos países de Europa y a la América del Norte.

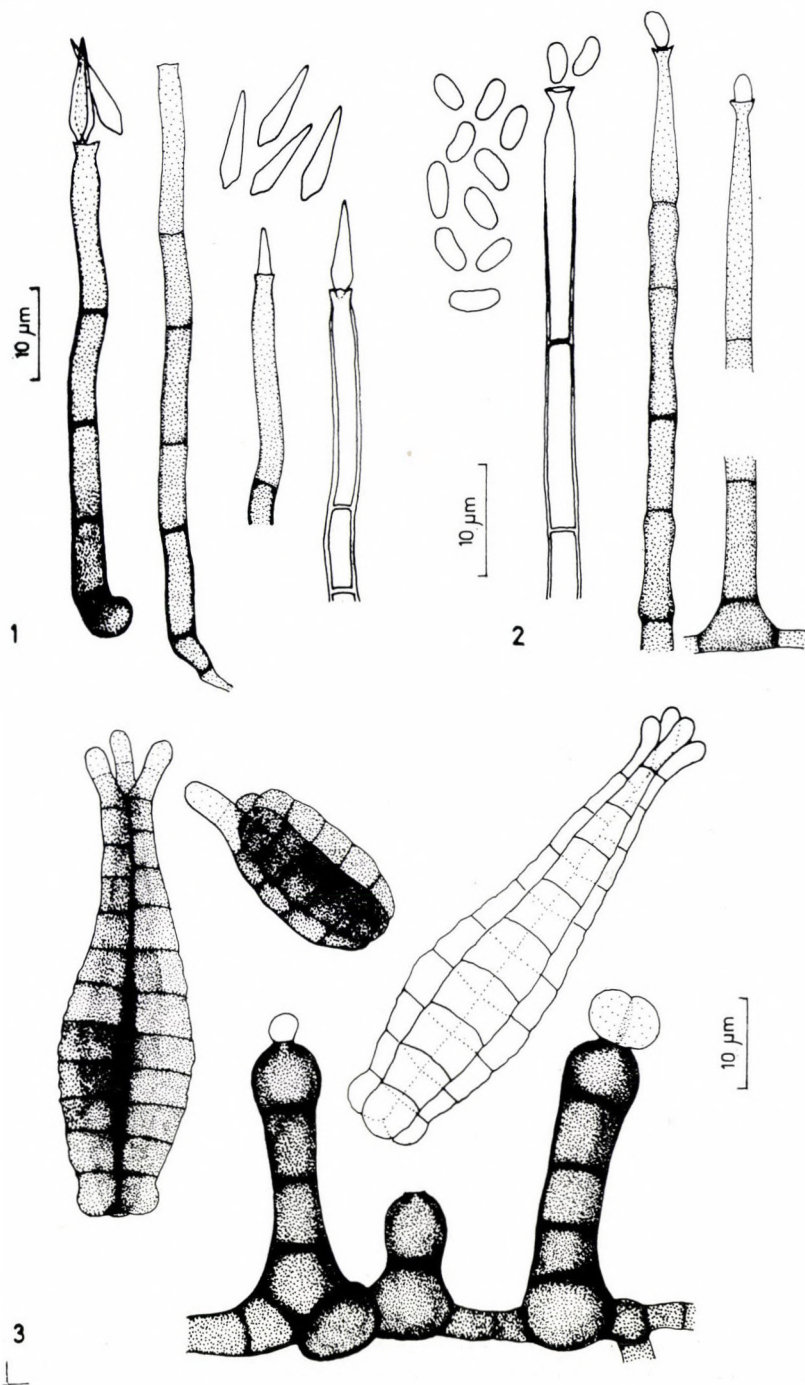
Chloridium obclaviforme Mena et Mercado spec. nov.*

Coloniae effusae, olivaceo-cinereo-brunneae, pilosae. Mycelium partim superficiale partim in substrato inmersum ex hyphis ramosis, septatis, pallide brunneis vel brunneis, laevibus, 2–2,5 μm crassis compositum. Conidiophora erecta, recta vel flexuosa, non ramosa, pallide brunnea vel brunnea suisum pallidiora, laevia, 25–80 μm longa, 2,5–3,5 μm crassa, 2,5–4,5 μm ad basem. Phialides ad 1,5–2 μm paulatim angustatae, collari dilatato, 2,5–3 μm crassa, 2–2,5 μm profundo terminatae, proliferatae. Phialoconidia in capitulis mucidis triangularibus aggregata, hyalina vel subhyalina, aseptata, obclavata, attenuata ad apicem. Cellula basalis cum papilla, laevia, 10,5–14 × (2–)2,5–3 μm.

Holotypus: in culmo lignescenti e mortuo putr. deiect. *Bambusae* sp. Los Llanos de Padilla, Topes de Collantes, Sancti Spíritus, Cuba. 2. II. 1983. A. MERCADO 7054 (HAC).

Colonias dispersas, pardas, gris oliváceas a pardas, pelosas. Micelio parte superficial, parte immerso en el substrato, compuesto de hifas ramificadas, septadas, pardo pálidas a pardas, lisas; 2–2,5 μm de grosor. Conidióforos erectos, rectos o flexuosos, sin ramificar, pardo pálidos a pardos, más pálidos hacia el ápice, lisos, 25–80 μm de longitud por 2,5–3,5 μm de grueso y 2,5–4,5 μm en la base. Fiálides que disminuyen su grosor gradualmente basta 1,5–2 μm y se expanden en un collarín acampanado, 2,5–3 μm de ancho, 2–2,5 μm de profundidad, con 0–2 proliferaciones percurrentes. Fialoconidios en cabezas mucilaginosas triangulares, hialinos a subhialinos, sin septos, estrechamente obclaviformes, atenuados hacia el ápice y con la base papilada, lisos; 10,5–14 × (2–)2,5–3 μm.

Holótipo: Sobre tallo muerto de *Bambusa* sp. Los Llanos de Padilla, Topes de Colantes, Sancti Spíritus, Cuba. 2. II. 1983. A. MERCADO 7054 (HAC).

Chloridium obclaviforme se distingue de las especies incluidas en el género por la morfología de los conidios. Esta especie presenta conidios estrechamente obclaviformes que son muy similares a los de la especie tipo del género *Phialogeniculata* MATSUSHIMA (1971). Las diferencias fundamentales entre este género que estableció MATSUSHIMA y *Chloridium* Link ex Fr. son la presencia en el primero de conidióforos con desarrollo marcadamente simpodial y conidios con un septo, en contraposición con el desarrollo mayormente percurrente de los conidióforos de *Chloridium*, excepto en la sección *Psilobotrys*

Lamina I

1. Chloridium obclaviforme spec. nova. Conidióforos, células conidiógenas con collarines y fialoconidios obclaviformes. *2. Chloridium lignicola.* Conidióforos, células conidiógenas fialídicas y fialoconidios. *3. Tretospeira ugadensis.* Conidióforos, células conidiógenas monotreticas y conidios

(Sacc.) W. Gams et Hol.-Jech., y la ausencia de septos en los conidios (GAMS y HOLUBOVÁ-JECHOVÁ 1976).

La especie que se propone en este trabajo como un nuevo taxon para la ciencia se caracteriza por poseer conidióforos que presentan proliferaciones percurrentes, fiálides integradas y conidios que surgen del interior de los collarines de las fiálides, sin septos y agrupados en cabezas mucilaginosas, por lo que consideramos que a pesar de la inusual morfología de los conidios su inclusión en el género *Chloridium* es correcta.

Codinaea lunulospora Hewings et Crane, Mycotaxon., 13: 401 (1981).

Sobre el peciolo y hojas muertas de *Roystonea regia* (H.B.K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7034 y 7043 (HAC).

Corynespora cassiicola (Berk. et Curt.) Wei, Mycological Pap., 34: 5 (1950).

Sobre el tallo y ramas muertas de *Arthrostylidium* sp. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7008 (HAC).

Helminthosporium foveolatum Patouillard, Journ. de Bot. Paris., 5: 321 (1891).

Sobre rama muerta de *Nectandra coriacea* (Sw.) Gris. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7049 (HAC).

Helminthosporium solani Dur. et Mont., Flore d'Algerie, Cryptogr., p. 356 (1849).

Sobre ramas muertas de *Fischeria havanensis* Deene. Pomarrosal de Leonila, Finca Cudina. 14. VII. 1982. A. MERCADO 6785 (HAC).

Sobre ramas muertas de *Ocotea leucoxylon* (Sw.) Mez. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7028 (HAC).

Helminthosporium velutinum Link ex Ficinus et Schubert, Fl. Geg. Dresd. krypt: 283 (1823).*

Colonias dispersas, negras, pelosas. Estroma presente. Conidióforos mayormente cespitosos, rectos o flexuosos, subulados, pardos muy oscuros a pardo negrozcos en la base, pardos hacia el ápice, lisos, hasta de 775 μm de longitud, 14–25 μm de grosor en la base, 8–12,5 μm en el ápice. Conidios rectos o flexuosos, obclaviformes, pardo pálidos a pardo dorados, con una cicatriz pardo negruzca en la base, lisos, con 7–12 seudoseptos; 45–70 $\times$ 15–20 μm, 5–7 μm de grosor en el ápice.

H. velutinum es muy común en las regiones templadas, aunque también ha sido encontrado en algunos países tropicales (ELLIS 1971). Es la primera vez que se colecta en Cuba.

Holubovaea roystonicola Mercado, Acta Botánica Cubana., 15; 7 (1983).

Sobre el pecíolo de la hoja muerta de *Roystonea regia* (H.B.K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7018 (HAC).

Menisporopsis theobromae Hughes, Mycol. Pap., 48: 59 (1952).

Sobre hojas muertas caídas; sobre ramas muertas de *Nectandra coriacea* (Sw.) Gris.; sobre el peciolo de la hoja muerta de *Roystonea regia* (H.B.K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7044, 7049, 7056 (HAC).

Stachylidium bicolor Link ex S. F. Gray: Link, Mag. Ges. Naturf. Fr. Berlin., 3 (1): 15 (1809); S. F. Gray, Nat. Arrangement British Plants, p 553 (1821); Fries, Syst. Mycol., 3: 391 (1832).

Sobre ramas muertas de *Trichostigma octandrum* L. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7016, 7045 (HAC).

Stachylidium cubense Mena et Mercado, Rev. Jardin Bot. Nac., 5 (3): 56–57 (1984).
Sobre ramas muertas de *Trichostigma octandrum* L. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7016, 7045 (HAC).

Tretospeira ugadensis (Hansf.) Pirozynski, Mycol. Pap., 129: 58–60 (1972).**

Sobre ramas muertas de *Coffea* sp. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7051 (HAC).

Colonias dispersas, negras, puntiformes. Micelio mayormente superficial, compuesto de hifas ramificadas, septadas, pardas a pardo oscuras, 3–7 μm de grosor. Conidióforos simples o en fascículos sueltos, erectos, rectos o ligeramente flexuosos, cilíndricos o estrechamente claviformes, con 3–4 septos, pardo oscuros; 25–40 × 6–7,5 μm. Células conidiógenas monotréticas, terminales, abultadas, 7–9 μm de diámetro. Conidios obclaviformes o estrechamente obpiriformes, con la base redondeada, gradualmente atenuados hacia el ápice, pardo dorados, rugosos, compuestos de 4 columnas de células unidas lateralmente, excepto hacia el extremo apical; 50–60 × 15–20 μm.

Los conidióforos del especimen cubano de *Tretospeira ugadensis*, tienen el ápice menos abultado que lo descrito por PIROZYNSKI (1972) para esta especie. Este hifomicete constituye un nuevo género para Cuba y con anterioridad sólo se había colectado en Tanzania y Uganda (ELLIS 1976).

Triadelphia stilboidea Mercado et Castañeda, Rev. Jardín Bot. Nac., 4 (2): 65–79 (1983).
Sobre el peciolo de la hoja muerta de *Roystonea regia* (H.B.K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7018 (HAC).

RECONOCIMIENTO

Agradecemos a la Dra. VERA HOLUBOVÁ-JECHOVÁ del Instituto de Botánica de la Academia de Ciencias de Checoslovaquia la revisión y opinión crítica acerca de algunos táxones aquí descritos.

REFERENCIAS

Ellis, M. B. (1971): *Dematiaceous Hyphomycetes.* Commonwealth Mycological Institute, Kew, Surrey, p. 608.
Ellis, M. B. (1976): *More Dematiaceous Hyphomycetes.* Commonwealth Mycological Institute, Kew, Surrey, p. 507.
Gams, W., Holubová-Jechová, V. (1976): *Chloridium* and some dematiaceous Hyphomycetes growing on decaying wood. *Studies in Mycology.*, **13.** Centraalbureau voor Schimmelcultures Baarn. p. 99.
Matsushima, T. (1971): *Microfungi of the Solomon Islands and Papua-New Guinea.* Kobe, Japan. p. 78.
Pirozynski, K. A. (1972): Microfungi of Tanzania. *Mycol. Pap.* **129:** 1–64.

Acta Botanica Hungarica 33 (1–2), pp. 81–103 (1987)

LM AND EM STUDIES ON POLLEN GRAINS OF RECENT *WELWITSCHIA MIRABILIS* HOOK. AND *EPHEDRA* SPECIES

M. Kedves

JÓZSEF ATTILA UNIVERSITY, DEPARTMENT OF BOTANY, SZEGED, HUNGARY

(Received: 15 April 1985)

LM, TEM and SEM studies on various maturity pollen grains of *Welwitschia mirabilis* Hook prepared by different methods have led to the following result: The tectum and infratectum when immature come off the foot layer and the characteristic sculpture is not seen. Dimorphism could not be pointed out for the pollen grains of the species. The characteristic sculpture of the region of colpus arranged in the direction of the polar axis can be studied first of all by SEM method. On the basis of the TEM results the pollen grain of *Welwitschia mirabilis* Hook. can be differentiated from the genus *Ephedra* by the absence of lamellar endexine. The differentiating character of the *Welwitschia* pollen often cannot be recognized by light microscope, so in the case of fossil pollen grains the two genera cannot always be differentiated with absolute certainty. In contrast with many earlier statements the pollen grains of the genus *Ephedra*, as opposed to the monocolpate pollen grain of *Welwitschia*, are polyplicate forms with several types within. Statistical examinations also succeeded in pointing out a characteristic dimorphism of pollen in a number of *Ephedra* species.

Introduction

The monotypic *Welwitschia* genus has been the subject of many investigations of various direction. According to the literary survey of Erdtman (1965) the first palynological data come from Fischer (1890). Erdtman (1965, p. 81) wrote the following: "The pollen grains in *Welwitschia* are very similar to those in *Ephedra*. The pollen grains in *Gnetum* are quite different." So the pollen studies in the genus *Welwitschia* are connected with those in the genus *Ephedra*. From the extremely rich literature on the pollen grains of *Welwitschia* and *Ephedra* we mention here some particularly important works: Wodehouse (1935), Bolkhovitina (1953) described the fossil genera: *Ephedripites*, *Welwitschiapites*. Cookson (1956) and Wilson (1959) dealt with further fossil forms. Beug (1956) pointed out the dimorphism of *Ephedra* pollen grains. Kremp (1965) contributed to the question by the following (p. 29): Steeves and Barghoorn, 1959, p. 227: "In the polar view the (*Ephedra* pollen) grains are polygonal with the alternating ridges and deep concave furrows forming an angular outline. A narrow and serpentine colpus is situated at the base of each furrow. In most cases the colpi are highly undulate. The undulation of the colpus may be either rounded or highly angular, and the frequency of undulation may vary, as well as the degree. The colpus may divide forming lateral branches which extend up the ridge where they may occasionally divide again. In this manner the ektexine forms a reticulate pattern, such as that found in *Ephedra* distachya. In a few cases, as in *E. clokeyi*, the colpus scarcely divides. Also, the width of the colpus may vary as well as the depth to which it cuts into the ektexine." P. 120: Erdtman, 1952, p. 467: "with ± colpoid grooves; a provisional term used in descriptions of the pollen grains of *Spathiphyllum* . . ." (Figs 289–300), *Ephedra* and *Welwitschia*". Afzelius (1956) published the first TEM data on the exine of *Ephedra monosperma*. Krutzsch (1961) wrote a

work of monograph character on the *Ephedripites* Bolkh. 1953 pollen grains of the Tertiary. E. NAGY (1963) contributed further data to the subject. DEÁK (1963) supporting the works by POTONIÉ (1958) and KRUTZSCH (1961) emphasized that the genus *Welwitschiapites* Bolkh. 1953 could not be brought into connection with the recent *Welwitschia* genus. BHARADWAJ (1963) wrote the following; p. 129: "Monocolpate, longitudinally and cross-striated pollen grains as described here for *Welwitschia* have not been frequently reported in fossil condition". GLADKOVA, SAUER and MTCHEDLISHVILI (1964) published data on the tetrads of *Ephedra*. SHAKHMUNDES (1964) described fossil *Ephedra* pollen grains in Palaeogene deposits of Western Siberia. POCOCK (1964) used the name *Equisetosporites* (DAUGHERTY 1941) POCOCK et JANS. emend. form-genus for the fossil "ephedroid pollen grains". He wrote of colpus that he placed in four types: (1) sinuous, (2) branching, (3) zigzag, (4) straigh. GULLVAG (1966) carried out TEM studies on the pollen grains of the genera *Gnetum*, *Welwitschia* and *Ephedra* and wrote the following (p. 445): "The electron microscopical evidence shows that the wall pattern of *Ephedra* and *Welwitschia* are as similar as can be expected from the study in the light microscope". KUVAEVA (1973) transferred several pollen grains described in the *Welwitschiapites* form-genus to the *Corniculatisporites* Kuv. 1971 and named the family Schizaeaceae as their botanical affinity. In her opinion the thickening at the poles suggests the spores of the genus *Appendicisporites* Weyl. et Krieg. 1953. Later KAR (1981) described the *Gondvastriatites* nov. gen. instead of the *Welwitschiapites*. M. VAN CAMPO and LUGARDON (1973) presented excellent TEM pictures of the exine of *Ephedra distachya* L. Under the tectum the infratectum is granular, the foot layer narrow, the endexine lamellar. In connection with the polarity of *Ephedra* pollen grains HUYNH (1974) pointed out the following (p. 473): "A study of the arrangement of the microspores of *Ephedra helvetica* in the tetrads shows that the longer axis lies in the equatorial plane of the pollen grain". In the course of LM and SEM studies on pollen grains of *Pteridophytes* and *Gymnospermatophytes* PLANDEROVÁ (1976) dealt with pollen grains of many recent *Ephedra* species as well as of *Welwitschia* too. In addition, several fossil taxa (*Ephedra* foss., *Vittatina*, *Gnetaceaepollenites*) were also taken under complex examination. TREVISAN (1980) carried out TEM studies on pollen grains of fossil *Ephedripites* too. ZHANG YU-LONG and XI YI-ZHEN (1983) examined Chinese recent pollen grains by LM and SEM methods. HESSE (1984) studied the pollen grains of *Ephedra campylopoda* C. A. Mey, *E. americana* Humb. et Bonpl. and *Welwitschia mirabilis* Hook. by TEM and SEM methods from the point of view of ontogeny, and found that the pollenkitt was absent in all three species. From a comparison with earlier data he drew the conclusion that the pollenkitt was an exclusive characteristic of the Angiospermae.

Present paper gives account of a complex study of the recent *Welwitschia mirabilis* Hook. aimed at disclosing the exact botanical relations of similar fossil pollen grains. Additional LM and SEM studies were carried out on several species of the genus *Ephedra*.

Material and method

Pollen grains of the recent *Welwitschia mirabilis* Hook. are not easily obtained even from African habitats.

Pollen preparations of this species as well as of a number of *Ephedra* species were sent by Dr. D. M. JARZEN (National Museums of Canada, Paleobiology Division, Canada). The methods and other information concerning the preparations are found in the publication of JARZEN (1977), the exchange catalogues are from JARZEN—WHALEN (1978) and WHALEN—JARZEN (1982). Acetolysed recent *Welwitschia* pollen preparation and fresh pollen material suitable for TEM and SEM studies were obtained from Dr. J. A. COETZEE (Institute for Environmental Sciences, The University of the Orange Free State, Bloemfontein, South Africa). The material was collected by M. HERRE from the botanical garden of the Stellenbosch University. Pollen grains without preparation (treated by three methods in total) were subjected to light microscope study. As for the acetolysis method we cite here UENO (1960,

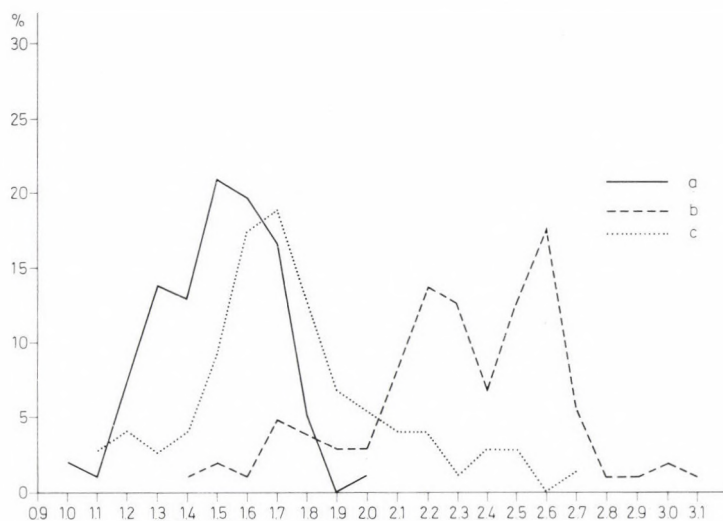



Fig. 1. Variation of longitudinal axis for pollen grains of *Welwitschia mirabilis* Hook. prepared in different ways; a = pollen grains without preparation, b = acetolysed pollen grains from Dr. J. A. Coetzee, c = acetolysed and stained pollen grains sent by Dr. D. M. Jarzen

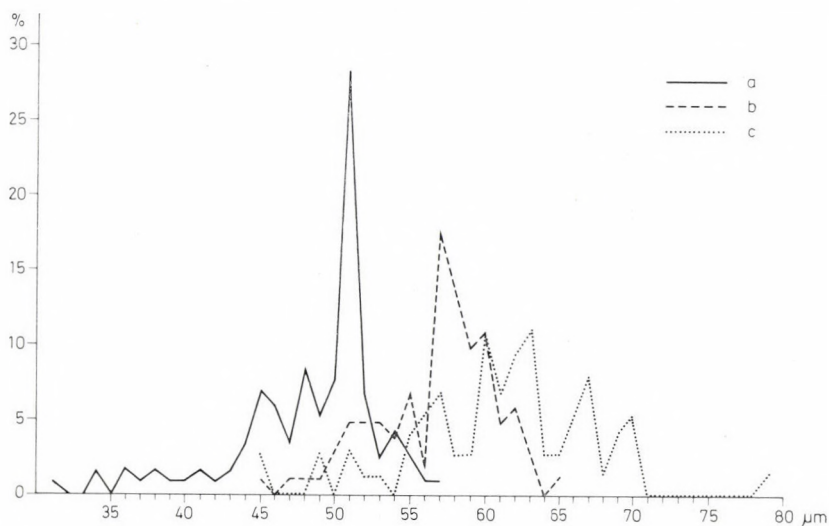



Fig. 2. Variation of the ratio of polar to equatorial axis of *Welwitschia mirabilis* Hook. pollen grains prepared in different ways; a = pollen grains without preparation, b = acetolysed pollen grains from Dr. J. A. Coetzee, c = acetolysed and stained pollen grains sent by Dr. D. M. Jarzen

p. 111): "a comfit type perine is readily lost from the surface and at the same time the granular structure of the sexine is altered seriously by acetolysis". For SEM examination pollen material of several recent *Ephedra* species was kindly sent by Dr. Lilla Hably from the Museum of Natural Sciences, Budapest. Measuring for the statistical evaluation of the light microscope examinations was performed by I. Gyuricza-Kollár. I express my thanks to all of them.

The TEM method of examination is in short the following: Fixation in glutaraldehyde, postfixation in OsO_4 (aqu. dil.), embedding in Araldit (Durcupan, Fluka). The ultrathin sections were made with a glass knife, and lead-citrate was used for contrasting. The pictures were taken with a TESLA-BS-50 electron microscope. The scanning electron microscope pictures were taken in the EM laboratory of the Institute for Biophysics in the Biological Centre of the Hungarian Academy of Sciences, on a JEM–ASID scanning supplement of a JEOL–100 B electron microscope. For the assistance given in the electron microscope technique thanks are due to Dr. Á. PÁRDUTZ and Dr. I. ROJIK.

Results

Welwitschia mirabilis Hook.

By the light microscope method the mature pollen grain (Plate I, 1–6) is found to be monocolpate, though this character is not distinct and often cannot even be noticed. The colpus sometimes widens at the ends (Plate I, 6). Appendix or thickening are not found at the poles. The pollen grain is striate, the number of muri is: 15–20. The longitudinal axis is 30–79 μm long, the percentage distribution of pollen grains of different length prepared with the three methods shows a considerable variation (Fig. 1). The ratio of longitudinal axis to width of the pollen grain is less varied (Fig. 2), in the case of samples obtained from the same site there is a certain similarity. In this context we refer to the results of M. VAN CAMPO (1947) who made some important statements concerning the biometrical method. For example, according to some authors the measuring results for a given species change. In her own studies she slightly modified the preparation technique and obtained two essentially different measurement variation curves for the pollen grains of *Cedrus libani*. Similarly interesting was the case when she measured 3×100 pollen grains in the same preparation, and the measurement variation curves of the three measurings were not totally identical. Pollen dimorphism could not be detected. With immature pollen grains the tectum and infratectum separate from the foot layer (Plate I, 7–10, Plate II, 1, 2), the characteristic features of the pollen grain often cannot be recognized, the surface is highly diversified. The SEM method made it possible to learn about many important characteristics (Plate II, 3, 4, Plate III, 1–3). The longitudinally arranged sculpture is a characteristic feature of the colpus region (Plate II, 3, 4, Plate III, 1, 2). The sculpture of the extragerminal surface is also better studied by the SEM method. According to our results of observation the separate tectum around the poles of not fully mature pollen grains forms a characteristic more or less circular structure (Plate III, 1, 2). Of the TEM results (Plate IV, 1–5) the following are remarkable: the texture of the ectexine is homogeneous, the infratectum is composed of tiny granules, in the vallae the tectum is characteristically crumpled (Plate IV, 2, 3), that is why the tectum together with the infratectum is readily detached from the foot layer.

Results of pollen grain studies in the genus Ephedra

The general morphological features of pollen grains in the genus *Ephedra* can be summarized as follows: 1. They are polyplicate pollen grains (Plate VI, 1, Plate VII, 15, 16). 2. They have several morphological types; 2.1. The surfaces of striae and vallae are more or less smooth (Plate V, 1–4); 2.2. The ridges are of undulate descent (Plate VIII, 3, 4). The pollen grain study of *Ephedra* species — while only of supplemental nature — was suitable for differentiating two morphological groups; 2.3. There are characteristic patterns (hyaline lines, zigzag) in the vallae (Plate VI, 1–4, Plate XI, 1–10, Plate XII, 1–7). 3. Pollen dimorphism with several types may also occur.

1 4 7

8

5

2

9

6

3

10

Plate I

Welwitschia mirabilis Hook., Light micrographs

1–6. Material for examination from Dr. D. M. Jarzen; 1602881, S. W. Africa, 124. *7, 8.* Material for examination from Dr. J. A. Coetzee; acetolysed pollen grain. *9, 10.* Material for examination from Dr. J. A. Coetzee; pollen grain without preparation. Magnification ×1000

1

3

2

4

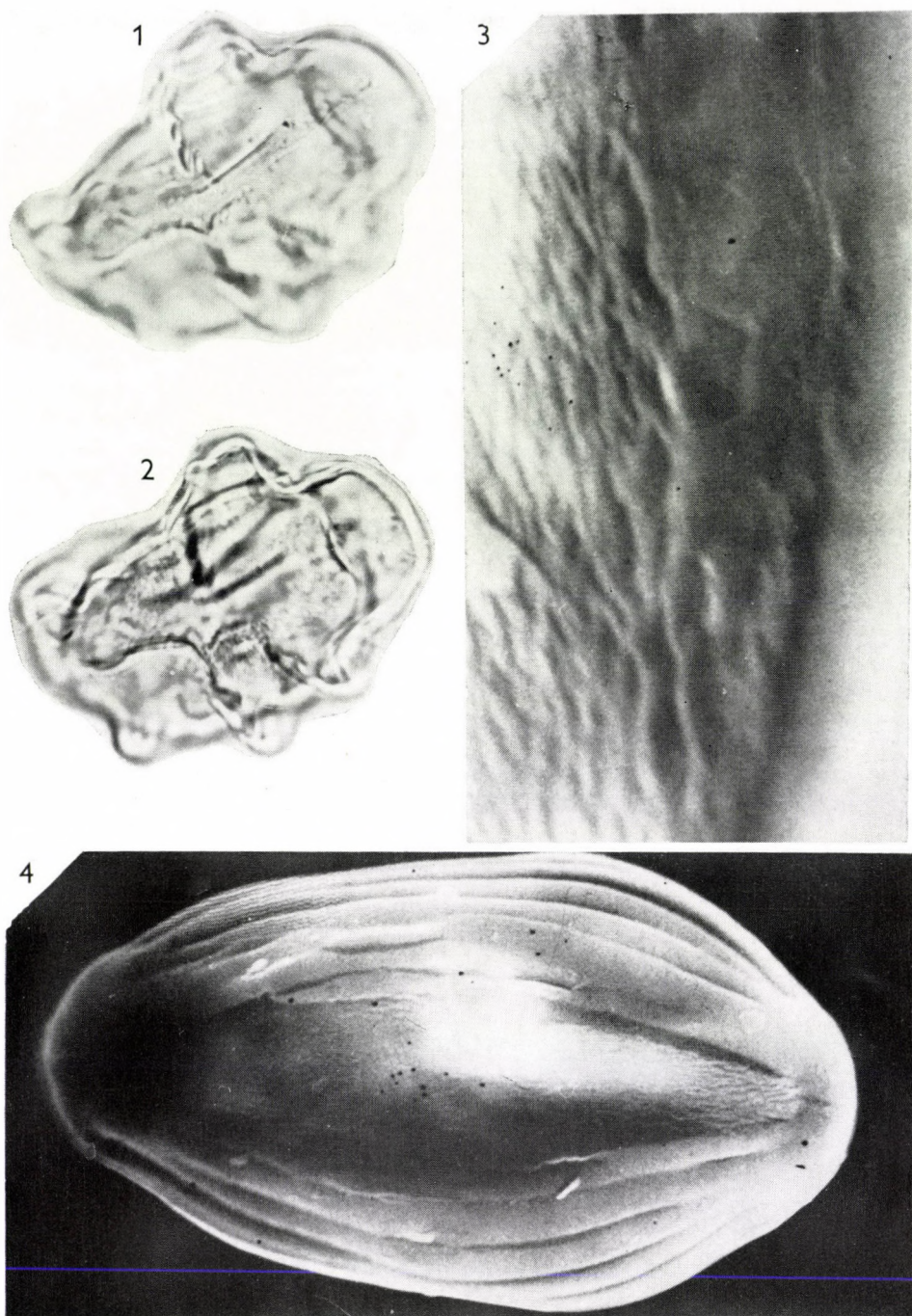



Plate II

Welwitschia mirabilis Hook.

1, 2. LM picture of pollen grain without preparation. Material for examination from Dr. J. A. COETZEE (×1000). *3.* Scanning electron microscope picture of the apertural region of pollen grain. The characteristic ornamentation round the colpus in the direction of the axis is clearly seen (×10 000). *4.* Comprehensive view of the surface of pollen grain. The difference in surface ornamentation between the apertural and extraapertural region is express (×2000)

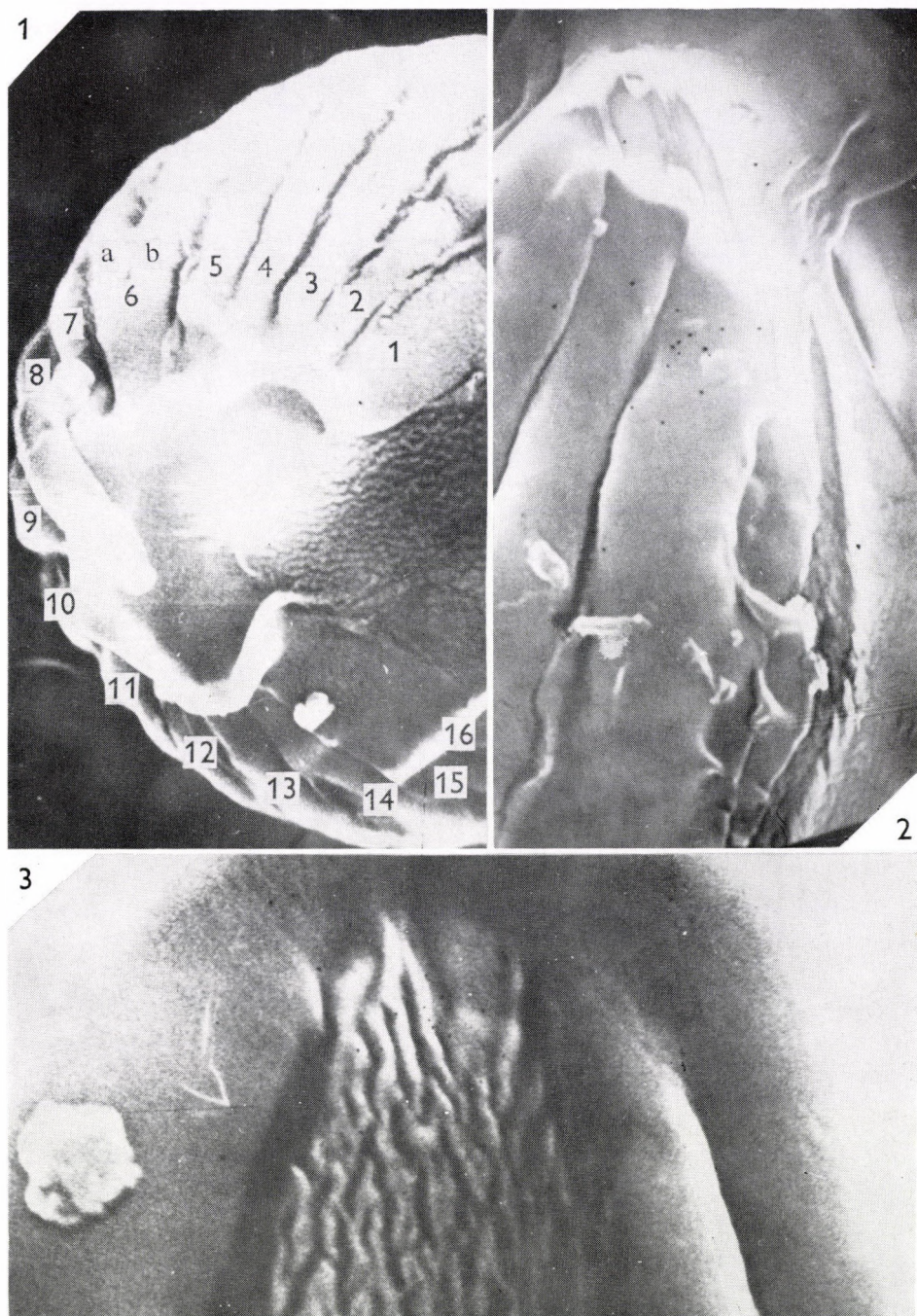
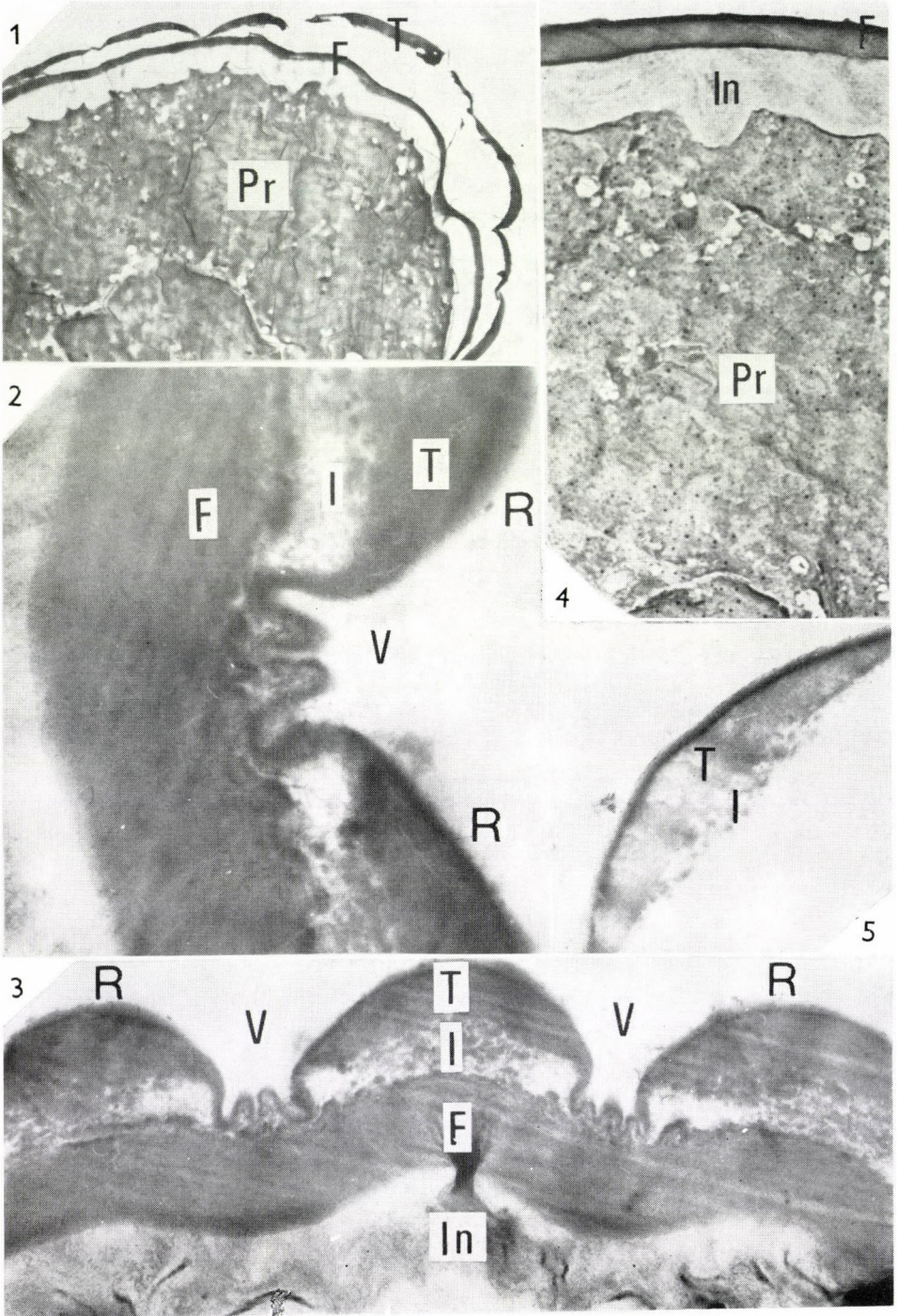



Plate III

Welwitschia mirabilis Hook. SEM pictures

1. Polar view of the surface of pollen grain (×3500). *2.* Apex of pollen grain from side view in the extraapertural region (×5000). *3.* Detail of the surface of apertural region near the pole (×10 000)

With the scanning electron microscope method the essential difference between the pollen grains of the *Welwitschia* and *Ephedra* genus can be unambiguously verifed. Namely, the colpus and the characteristic colpus region of the pollen grain are lacking in the genus *Ephedra*. In this respect highly valuable are the photos made in polar view (e.g. Plate VI, 1) which clearly show that all ridges and vallae, respectively, are equal in value.

The studies on the pollen grains of the genus *Ephedra* were of supplemental character, and though they were not aimed at completeness we hope that the data given below will be found useful for comparison in studies on fossile forms.

1. The pollen grains of the species below are characterized by the following morphological features: (1) Pollen dimorphism could not be detected by light microscope. (2) The ridge is of straight descent and the vallae do not show tracery.

1.1. *Ephedra trifurica* Torr. ex Wats. (Plate VII, 1–4)

The longitudinal axis is 36–60 μm, the measuring data (on the basis of 201 specimens) suggest two maxima, at 46 and 51 μm, respectively. The ratio of polar to equatorial axis is 1.1–3.4, here again two maxima are largely seen, at 2.2–2.5 and 2.8, respectively. The thickness of the exine is 0.5–1.2 μm on the sides and 1–2 μm at the poles. The vallae and ridges, respectively, are 10–12–16 in number.

1.2. *Ephedra antisyphilitica* C. Meyer (Plate VII, 5–8)

The longitudinal axis is 34–67 μm with an extended maximum between 51 and 55 μm. (Measuring data are based on 144 specimens.) The ratio of polar to equatorial axis is 1.4–3.6, the highest values are found between 2.0 and 2.5; 2.0 (10.8%), 2.1 (7.9%), 2.3 (11.5%), 2.4 (10.8%), 2.5 (12.2%). The thickness of the exine both on the sides and at the poles is around 1 μm. The vallae and ridges, respectively, are 10–12–14 in number.

1.3. *Ephedra torreyana* C. Wats. (Plate VII, 9–12)

The longitudinal axis is 28–47 μm, the maximum — an outstanding one (21.8%) — is at 43 μm. (Measuring data are based on 109 specimens.) The ratio of polar to equatorial axis is 1.1–3.3, the highest percentages are found between 2.1 and 2.6: 2.1 (8.2%), 2.2 (10.0%), 2.3 (8.2%), 2.4 (13.6%), 2.5 (9.1%), 2.6 (14.5%). The thickness of the exine is around 1.0 μm on the sides and at the poles alike. The vallae and ridges are 6, 7 in number.

←

Plate IV

Welwitschia mirabilis Hook., TEM pictures

1. Comprehensive view of an ultra-thin section of a not fully mature pollen grain. Separation of some layers of exine is clearly seen (×2000). *2.* Detail of the ultrastructure of ectexine in mature pollen grain. The tectum in the vallae is characteristically bent back, the infratectum granular (×50 000). *3.* Detail of the fine structure of exine in mature pollen grain. No endexine under the foot layer, the intine granular (×25 000). *4.* Submicroscopic structure of foot layer, intine and protoplasm. Tectum and infratectum detached (×5000). *5.* Fine structure of detached tectum and infratectum (×10 000). T = tectum, I = infratectum, F = foot layer, In = intine, Pr = protoplasm, St = striae, R = ridge

1 3 2 4

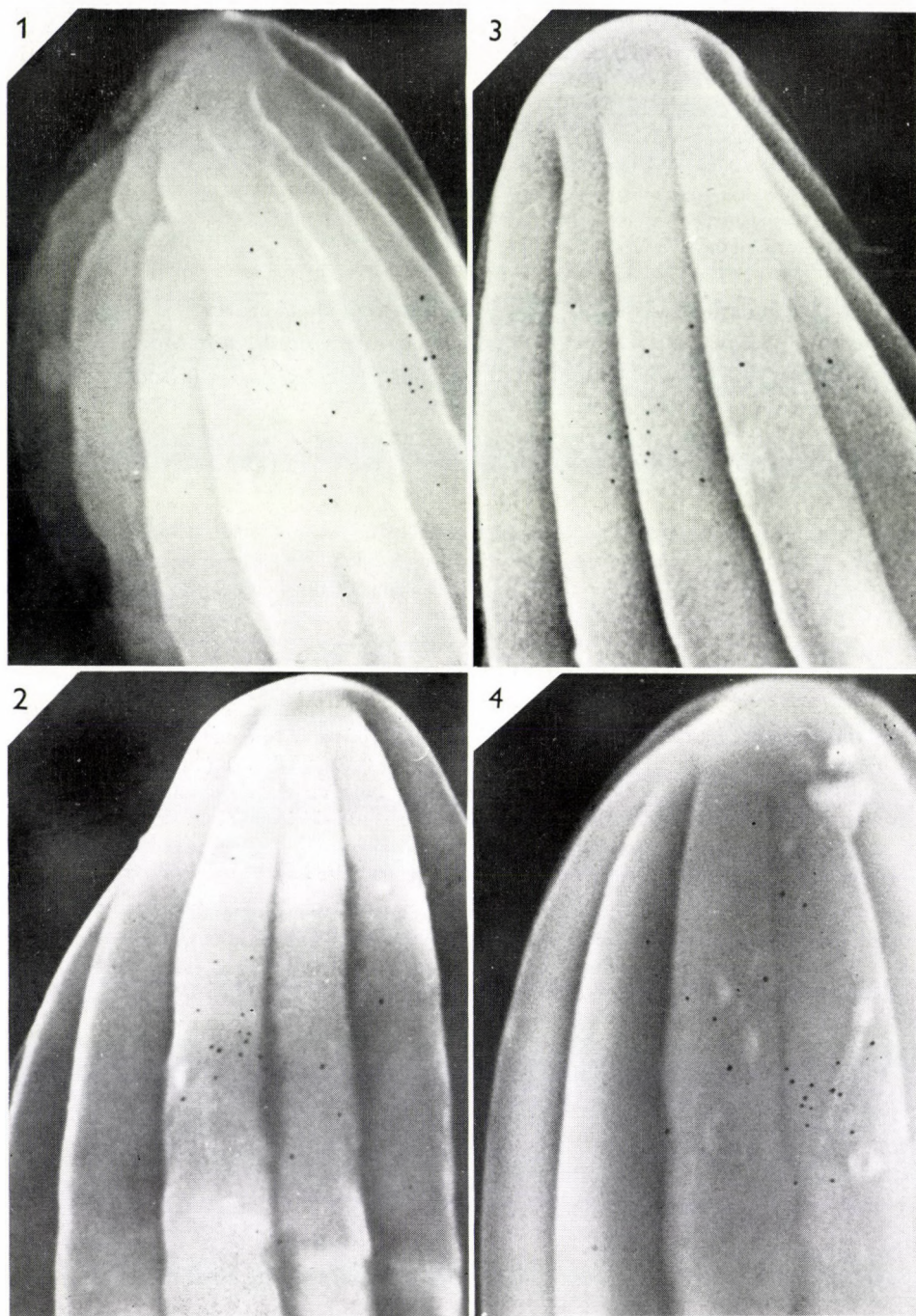



Plate V

SEM pictures of pollen grains from *Ephedra* species. Material for examination from Dr. LILLA HABLY

1. Ephedra fragilis Desf., Arboretum Kas Fr., Herbarium Vadense 209/120, 1933, leg.: G. H. RUISCH. *2. Ephedra californica* Wats. Herbarium Vadense 209/104. *3. Ephedra alata* Dcne., Sandy desert between Khidr al Ma'i and Towai al Mushaish in Southern Desert. 24. 3. 1957, leg.: K. H. REICHINGER. *4. Ephedra strobilacea* Bge., Iran, 23. 6. 1980 (×5000)

1

2

3

4

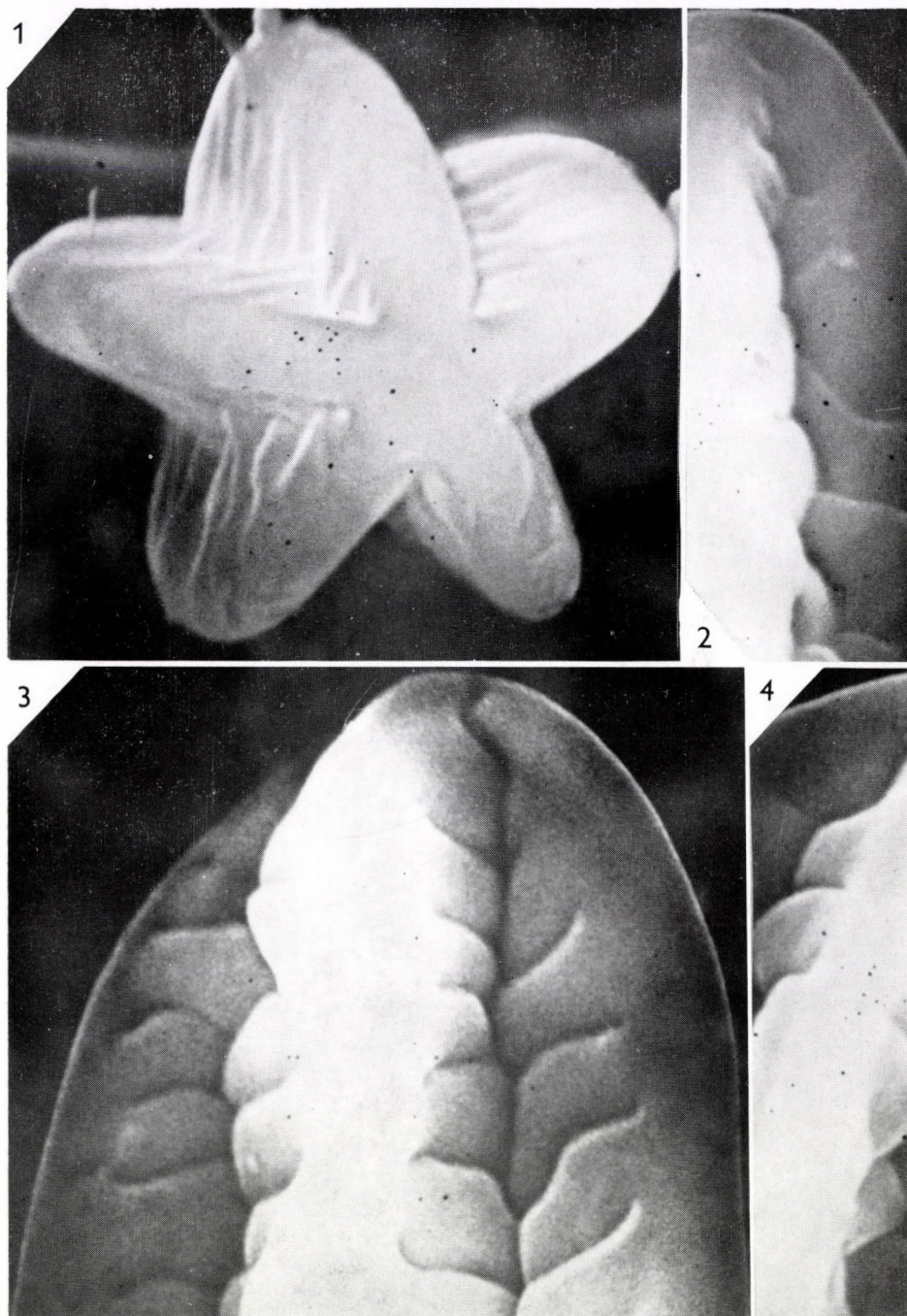



Plate VI

SEM pictures of pollen grains from *Ephedra* species. Material for examination from Dr. Lilla Hably

1, 2. Ephedra intermedia Schrenk et C. A. Meyer, Iran, 23. 6. 1980. *3, 4. Ephedra procera* C. A. Meyer, Iran, 23. 6. 1980 (×5000)

1 2 7 11 12 13 14 3 4 8 15 9 5 6 10 16

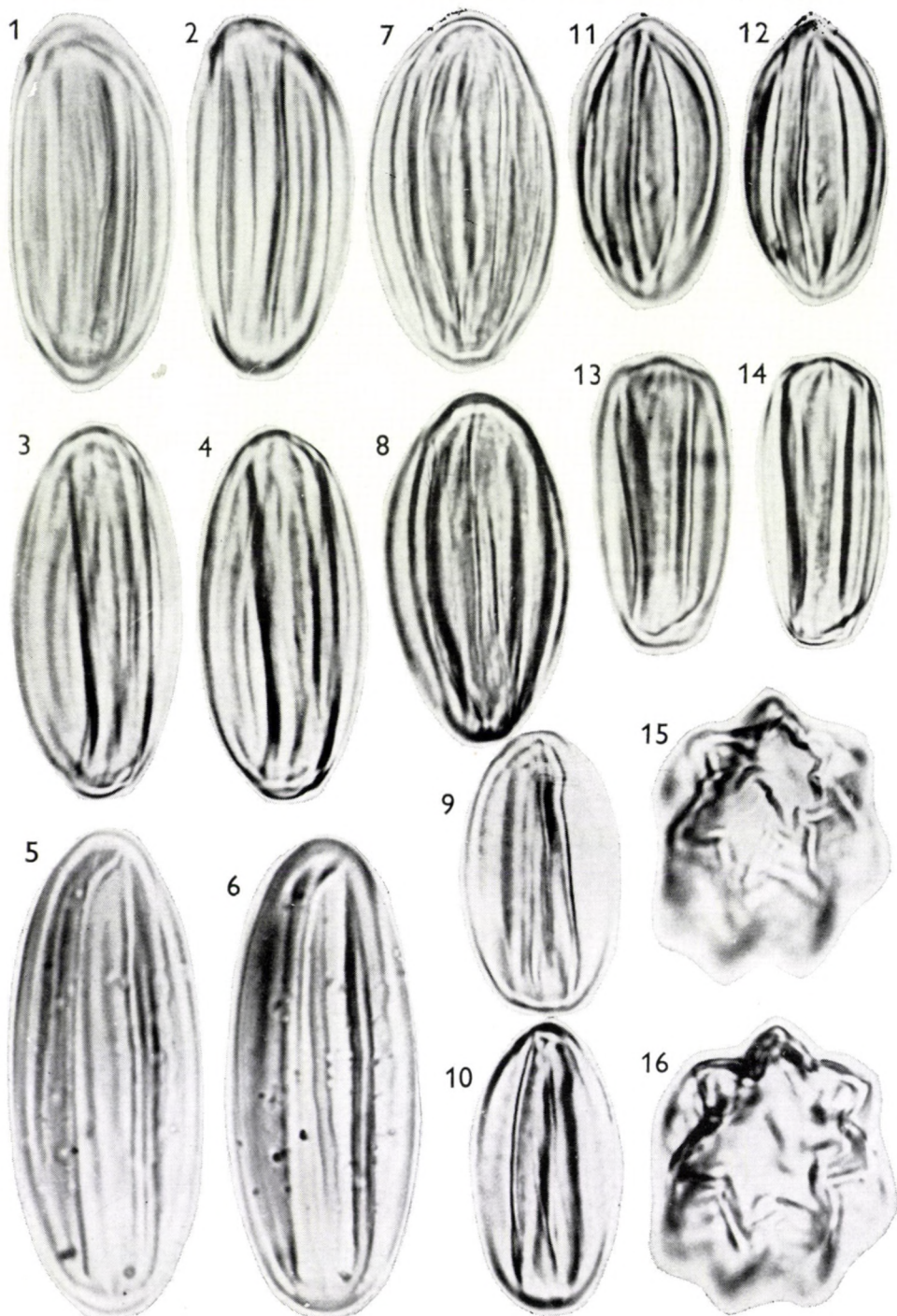



Plate VII

Light micrographs of pollen grains from *Ephedra* species.
Material for examination from Dr. D. M. JARZEN

1–4. Ephedra trifurcata Torr. ex Wats., 182, MO 1096753, USA, AZ. *5–8. Ephedra antisyphilitica* C. Meyer, 178, MO 80291, USA, TX. *9–12. Ephedra torreyana* C. Wats., 181, unknown. *13–16. Ephedra nana* Dusen., 189, MO 979559, Argentine, Patagonia (×1000)

1.4. *Ephedra nana* Dusen (Plate VII, 13–16)

The longitudinal axis is 23–44 μm long with several maximum values at 33 μm (14.2%), 36 μm (13.1%), 38 μm (12.5%). (Measuring data are based on 176 specimens.) The ratio of polar to equatorial axis is 1.1–3.6, with several maxima again: 1.9 and 2.0 (13.0%), 2.2 (11.4%), 2.5 (7.4%). The thickness of the exine is 0.6–0.9 μm both on the sides and at the poles. The vallae and ridges, respectively, are 7–8–10 in number. The photos 15 and 16 in Plate VII taken of the pollen grain from a polar view clearly show it.

2. The pollen grains of the following species are characterized by definite pollen dimorphism.

2.1. *Ephedra ochreata* Miers (Plate VIII, 1–4)

The dimorphism is equally manifest in the size and in the qualitative features. Larger specimens occurred in 57.9, smaller ones in 42.1 per cent. (The measuring data are based on 202 specimens.) The size of the larger specimens was between 38.0 and 63.0 μm, while that of the smaller ones ranged from 27.0 to 51.0 μm; the maxima were at 51.0 and 34.0 μm, respectively. The ratio of polar to equatorial axis is 1.2–3.3, the maxima are: 1.3–1.5 (7.4%, 12.8%, 12.4%), and 1.8–2.1 (6.9%, 4.9%, 7.9%, 7.4%). The ridges of the larger specimens — 8–10–12 in number — are of straight descent. The thickness of the exine both on the sides and at the poles is 0.9–1.4 μm. The smaller specimens have highly undulate ridges, 8–12–16 in number. The thickness of the exine is 0.7–1 μm on the sides and 1.5–1.8 μm at the poles, that is at the tips of the pollen grain a slight thickening is seen.

2.2. *Ephedra americana* H. et B. (Plate VIII, 5–8)

In this species again the dimorphism of the pollen grain is manifest in the size of the longitudinal axis and in the qualitative features alike. (The measuring data are based on 189 specimens.) On the other hand, as for the percentage proportions of the two kinds of pollen grain the difference compared to the former species is remarkable; the larger pollen grains occurred in 91.6, the smaller ones in 8.4 per cent. The polar axis was 41.0–63.0 μm for the larger specimens, with a maximum at 51.0 μm, and 30.0–46.0 μm long for the smaller ones, those with a 35.0–38.0 μm long axis occurred in the highest proportion. The ratio of polar to equatorial axis was 1.3–3.5, specimens of the 1.9–2.1 interval were found in the largest number (11.1%, 13.8%, 9.5%). The ridges of the larger specimens — 10–12 in number — generally were of straight descent, only seldom slightly undulate. The thickness of the exine 1.0–1.8 μm on the sides and at the apices alike. The ridges of the smaller specimens were consistently undulate, though this characteristic was not as expressed as in the former species. The ridges were 10, 12 in number. At the poles the pollen grain was somewhat thickened — 2.5–3.4 μm — compared to the 2.0–2.6 μm thickness of the exine on the sides.

2.3. *Ephedra tweediana* Fisch. et Meyer (Plate VIII, 9–12)

The pollen dimorphism is, in essentials, the same here as in the above discussed species. (Measuring data are based on 205 specimens.) Larger pollen grains occurred in 94.0, smaller ones in 6.0 per cent. The polar axis of the larger specimens was 36.0–60.0 μm long, the maximum with 51.0 μm, that of the smaller ones was 23.0–43.0 μm, specimens 33.0 μm in length were found in the highest percentage. The ratio of polar to equatorial axis was 1.1–3.4; specimens between 1.8 and 2.4 occurred in the largest number (10.2%, 7.3%, 9.3%, 11.7%, 9.3%, 6.3%, 5.8%). The larger specimens — 10–12 in number — had ridges of straight descent.

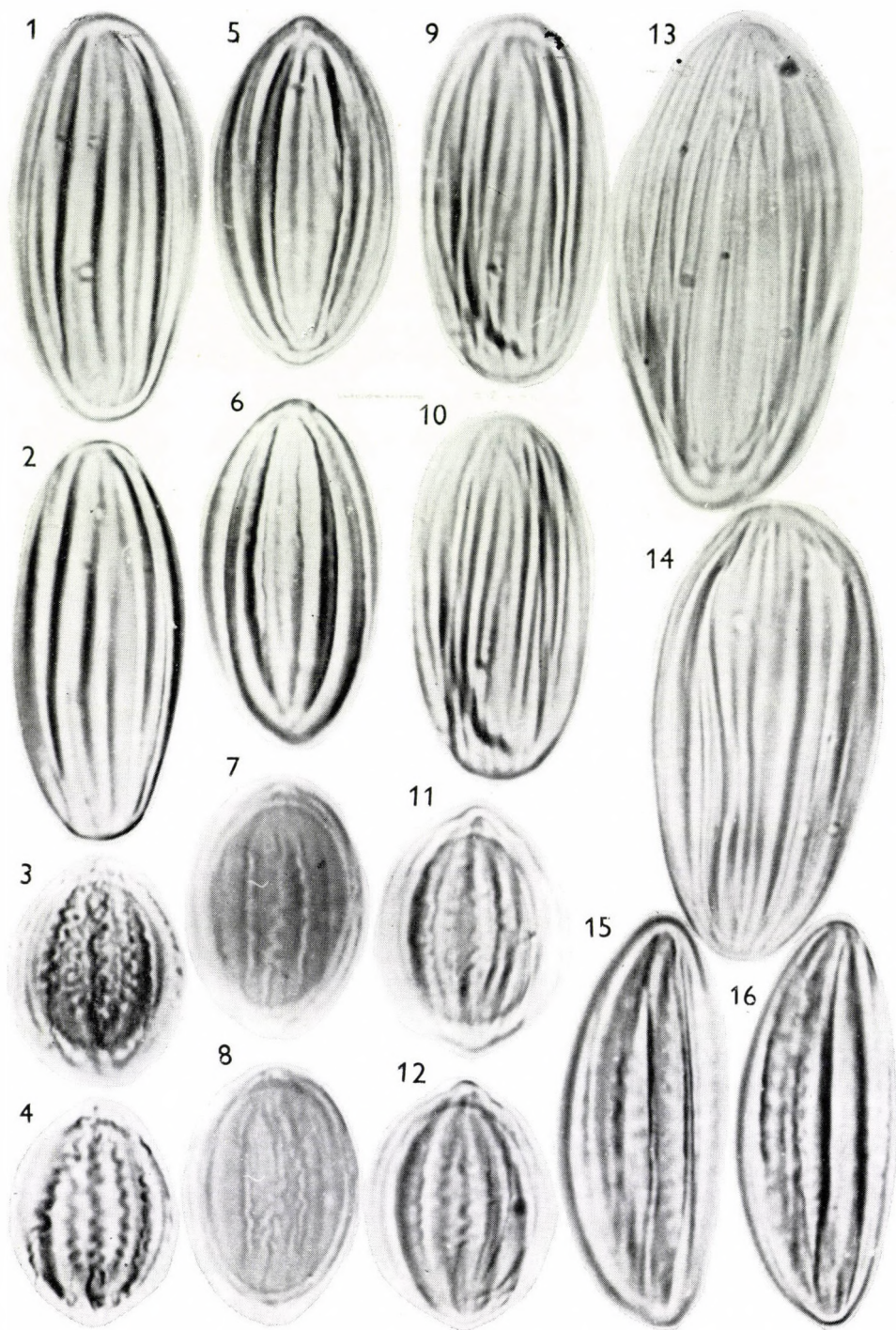



Plate VIII

Light micrographs of pollen grains in *Ephedra species.*
Material for examination from Dr. D. M. Jarzen

1–4. Ephedra ochreata Miers, 9268, MO 1598826, Dept. Agriculture, Ottawa, Canada 4365, Argentine, Mendoza. *5–8. Ephedra americana* H. et B., 9266, MO 1789212, Hutchinson, P. C. 1691, Peru, Ayacaha. *9–12. Ephedra tweediana* Fisch. et Meyer, 9269, MO 2624782, Peterson, E. et al. 1696, Argentine. *13–16. Ephedra aphylla* Forsk., 9272, MO 2207358, Abdallah, M. et al. 1370, United Arab Emirates (×1000)

The thickness of the exine 1.3–1.8 μm both at the poles and on the sides. The ridges of the smaller specimens — 10–12–14 in number — were highly undulate. At the poles the exine was thicker — 2.5–3.6 μm — compared to 2–2.4 μm on the sides.

2.4. *Ephedra aphylla* Forsk. (Plate VIII, 13–16)

The dimorphism of pollen grains agrees in essentials with that in the former species, but the difference in size and qualitative features is not so expressed in this species. (Measuring data on the basis of 169 specimens.) Furthermore, the number of smaller specimens with sculptured ridges is very low, lower than 1 per cent, so the quantitative data practically refer to pollen grains mentioned earlier as larger specimens. The polar axis is 51.0–82.0 μm long, specimens between 68.0 and 73.0 μm occurred in the highest percentage (10.6%, 10.6%, 8.9%, 7.7%, 5.3%, 7.1%). The so-called smaller specimens cannot be evaluated from this point of view; those between 50.0 and 60.0 μm could be observed. The ridges of specimens occurring in masses are of straight descent, 12–16–18 in number. The exine both on the sides and at the poles is 2.0–3.0 μm thick. The ridges of the smaller specimens are generally 8 in number; as opposed to the former there are coarctations at the bases of the ridges which give the characteristic sculpture of the pollen grain. Thickening could not be observed at the poles; the exine is 1.6–2.0 μm-thick.

2.5. *Ephedra alata* Decne (Plate IX, 1–4)

The pollen dimorphism in this species is again expressed. The larger pollen grains occurred in 83.0, the smaller, the ornamented ones in 17.0 per cent. (The measuring data are based on 200 specimens.) The polar axis of the larger specimens is 42.0–77.0 μm, the majority is about 63.0–69.0 μm (9.5%, 5.0%, 4.5%, 5.5%, 8.0%, 6.5%, 8.5%), the smaller ones are 43.0–72.0 μm long, 62.0 μm with most of them. So the difference in size between the two types of pollen grain is not so definite as with the earlier discussed specimens (2.1., 2.2., 2.3.). The ratio of polar to equatorial axis is 1.5–3.5, 2.0–2.4 and 2.6 in the highest percentage (8.5%, 9.5%, 9.0%, 9.5%, 9.0%, 9.0%). The ridges of the larger specimens are straight in descent, very seldom slightly undulate at the base; they are 10–12–16 in number. The exine is 1.0–1.8 μm thick on the sides and at the poles alike. With the smaller, ornamented specimens the ridges and their bases may equally be undulate; the ridges are 8, 10 in number. No remarkable thickening at the poles could be observed, the thickness of the exine is about 0.8–1.0 μm.

2.6. *Ephedra breana* Phil. (Plate IX, 5–10)

The pollen grains of this species are highly similar to those discussed in the foregoing except that the smaller specimens only occurred in 3.5 per cent. (Measuring data are based on 176 specimens.) The polar axis of the larger pollen grains is between 45.0 and 81.0 μm in length, 69.0 μm for the highest percentage. The smaller ones are 39.0–55.0 μm long, so the differences in size are rather remarkable. The ratio of polar to equatorial axis is 1.3–3.3, some of the quotients occurred in high percentages: 1.8 = 10.2%, 2.0 = 9.7%, 2.1 = 11.9%, 2.2 = 8.5%, 2.4 = 8.0%, 2.6 = 8.5%. The ridges of the larger specimens — 14–16–18 in number — are straight in descent. The exine is 1.8–2.5 μm thick both on the sides and at the apices. With the smaller specimens the ridges are about 14 in number, their descent is slightly undulate; the thickness of the exine is in general, 1.0–1.5 μm.

2.7. *Ephedra andina* Poepp. (Plate IX, 11; Plate X, 1–5; Plate XI, 1, 2)

This species somewhat differs from the former ones as regards pollen dimorphism. Ornamented pollen grains with undulate ridges occur in 67.5 per cent, thus — as opposed to those discussed above — they outnumber by far the specimens with smooth ridges. (Measur-

1 5 6 9

2 7 10

3 4 8 11

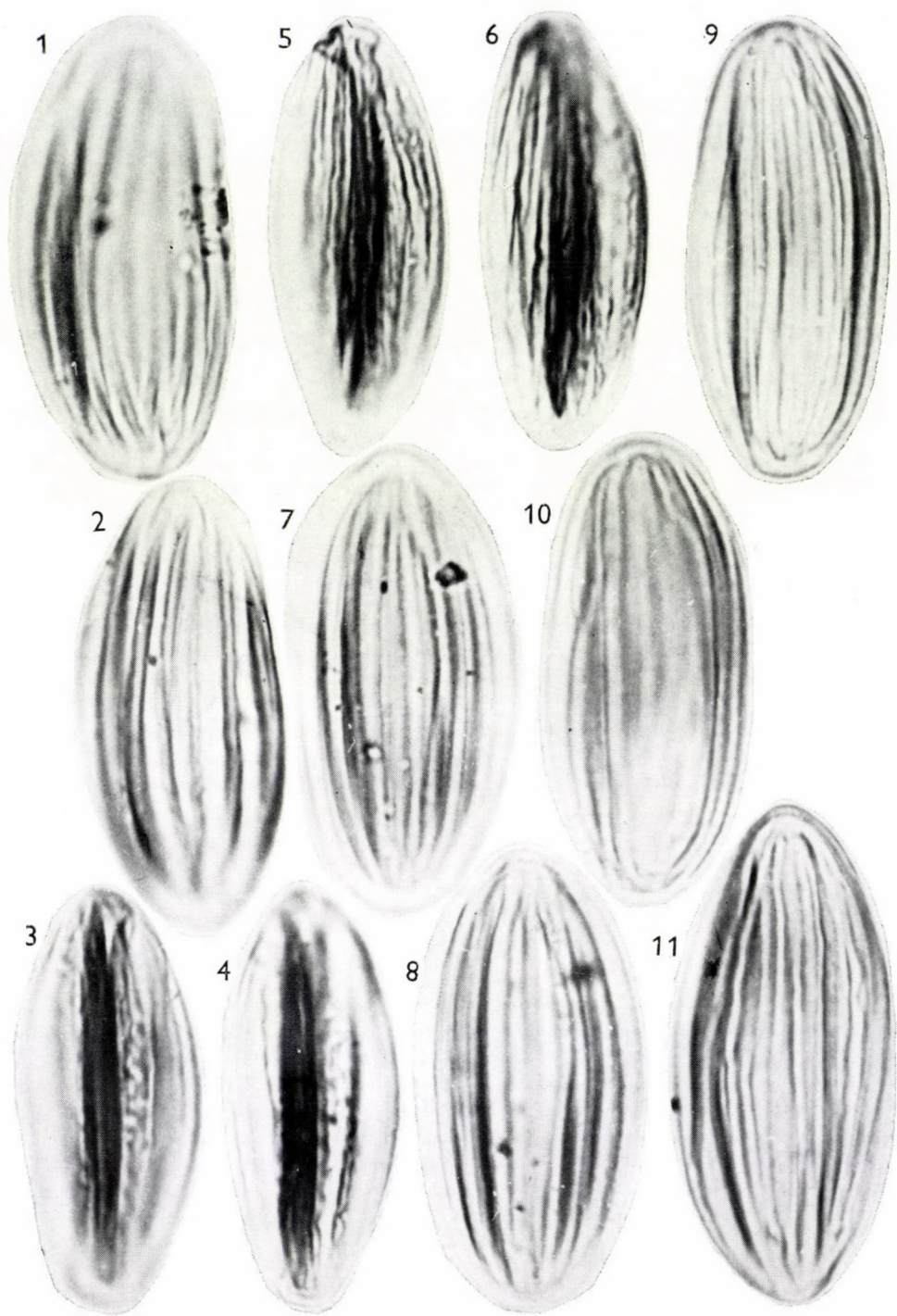



Plate IX

Light micrographs of pollen grains in *Ephedra* species.
Material for examination from Dr. D. M. JARZEN

1–4. Ephedra alata Decne, 9271, MO 2053668, Ibrahim et Mahdi, Egypt, Cairo. *5–10. Ephedra breana* Phil., 9267, MO 2747158, Zollner, O. 10278, Chile, Atacama, Breas. *11. Ephedra andina* Poepp., 9265, MO 1306161, Aravena, P. 33345, Chile, Curico (×1000)

1

2

3

4

5

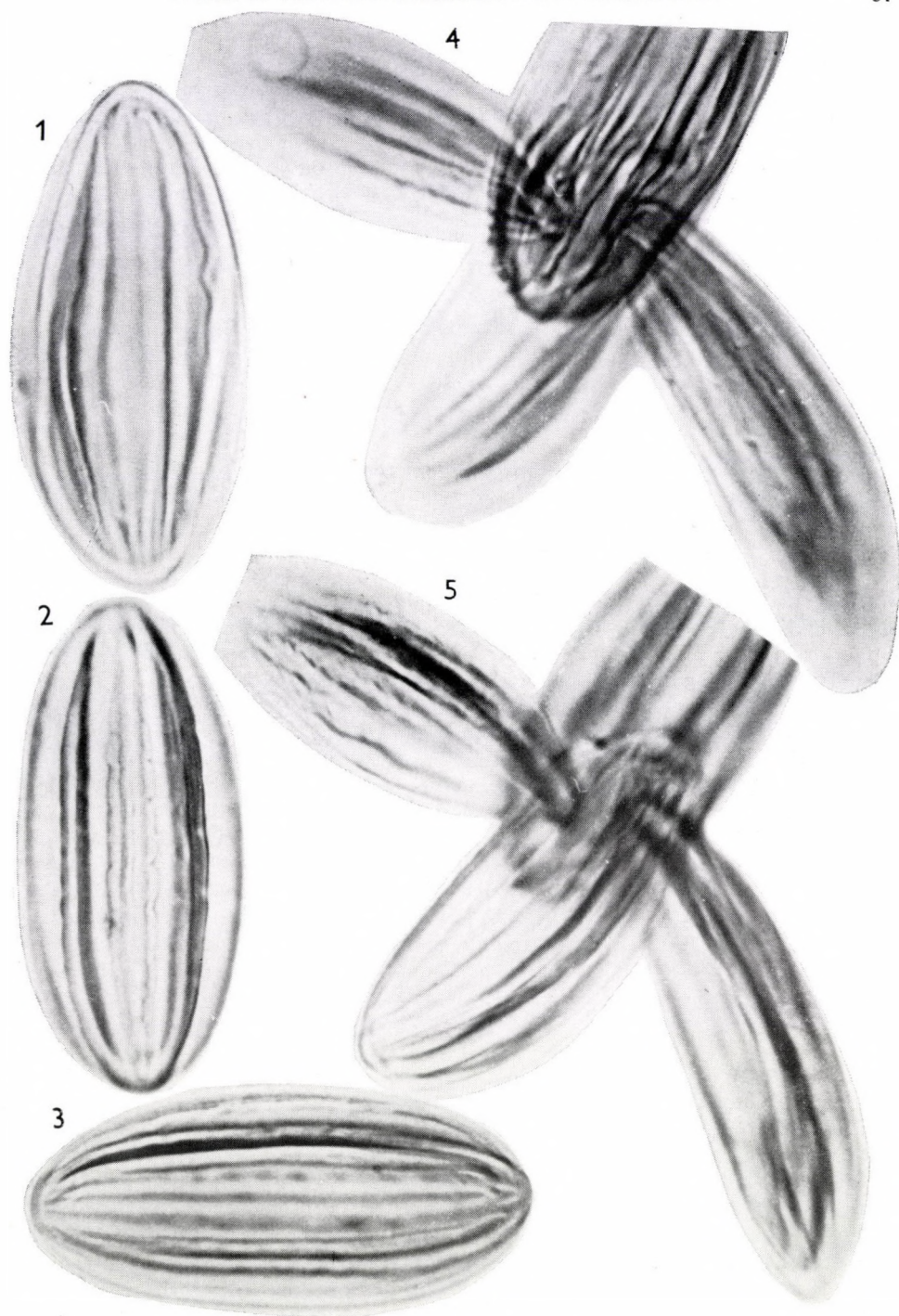



Plate X

Light micrographs of pollen grains in *Ephedra* species.
Material for examination from Dr. D. M. JARZEN
1–5. Ephedra andina Poepp., 9265, MO 1306161, Aravena, P. 33345, Chile, Curico (×1000)

ing data are based on 201 specimens.) Besides, pollen grains ornamented in the vallae also occurred, though in a minimum proportion. Further, the situation is just the opposite as regards the length of the polar axis too. The polar axis data of pollen grains with undulate ridges are: 36.0–82.0 μm, maximum: 11.4% with 69.0 μm; while those for pollen grains with smooth ridges are: 60.0–75.0 μm, maximum with 69.0 μm; the size of specimens ornamented in the vallae is largely the same. The ratio of polar to equatorial axis is 1.3–3.9, 2.2 for the maximum proportion (16.9%). The number of ridges: 8–10–12 with all kinds of pollen grain; thickening at the apices was not observed. The exine is 1.8–2.4 μm thick.

3. As a main common feature the pollen grains below have characteristically ornamented (zigzag, hyaline lines) vallae.

3.1. *Ephedra clokey* Cutler (Plate XI, 3, 4)

As to the morphology of pollen it is a uniform species. The polar axis is 51.0–75.0 μm long, some lengths occur in relatively high percentages: 63.0 μm in 11.8%, 65.0 μm in 8.3%, 66.0 μm in 7.3%, 67.0 μm in 11.3%, 69.0 μm in 10.3%. (Measuring data are based on 204 specimens.) The ratio of polar to equatorial axis is 1.3–3.8; ratios occurring more frequently are: 2.2 = 8.3%, 2.3 = 10.8%, 2.4 = 8.8%, 2.5 = 7.8%, 2.6 = 12.2%, 2.7 = 7.3%, 2.8 = 6.9%, 2.9 = 7.3%. The number of ridges generally is 5; in the middle of the wide vallae zigzag, hyaline lines caused by a partial thinning of the ectexine are found. These lines consist of a central part and simple branches. The branches are 4–6 μm apart, each is 3–5 μm long. There is no thickening at the apices, the exine generally is 2–3 μm thick.

3.2. *Ephedra aspera* Engelm. (Plate XI, 5–8)

Similarly to the former species it is uniform from the point of view of pollen morphology with the only difference that in this species slightly twisted forms also occur (Plate XI, 5, 6), though in a minimum quantity. The polar axis is 34.0–70.0 μm long, two lengths occur with a relative frequency: 51.0 μm in 10.9%, 57.0 μm in 10.1%. (Measuring data are based on 119 specimens.) The ratio of polar to equatorial axis is 1.2–3.7, those occurring in higher percentages are: 1.9 = 7.6%, 2.3 = 8.4%, 2.4 = 6.7%, 2.5 = 9.2%, 2.6 = 8.4%, 2.8 = 6.7%. The number of vallae generally is 7. The characteristic zigzag design shows a simple branching pattern, the branches are 2–3 μm long each and are 2–4 μm apart. There is no thickening at the apices, the thickness of the exine is 1.5–2.0 μm.

3.3. *Ephedra coryi* Reed var. virgata (Plate XI, 9, 10; Plate XII, 1–3)

As opposed to the former two species strict spiral are also encountered here, and that in 6 per cent. (Measuring data are based on 175 specimens.) The typical forms have 50.0–93.0 μm long polar axes, and in an interesting way none of the lengths or length intervals occur in outstanding percentages. The spiral forms are 69.0–88.0 μm in length, so this character is the property of the larger specimens. The ratio of polar to equatorial axis is 1.2–3.7; the following ratios are found in higher percentages: 2.3 = 8.4%, 2.4 = 6.7%, 2.5 = 9.2%, 2.6 = 8.4%, 2.8 = 6.7%. The ridges generally are 6 in number. The vallae mostly show a simple branching design, although the lateral branches sometimes may branch off again, or two lateral branches start from the same point of the main branch. The branches are at a distance of 2–3.5 μm from one another, the lateral branches are 3.5–5.0 μm long each. Thickening was not observed at the apices, the exine generally is 2.0–2.6 μm thick.

1 5 6 9 2 7 10 3 4 8

Plate XI

Light micrographs of pollen grains in *Ephedra* species.
Material for examination from Dr. D. M. Jarzen
1, 2. Ephedra andina Poepp., 9265, MO 1306161, Aravena, P. 3345, Chile, Curico. *3, 4. Ephedra clokeyi* Cutler, 180, MO 1032272, USA, CA. *5–8. Ephedra aspera* Engelm. ex Wats., 179, MO 80281, unknown. *9, 10. Ephedra coryi* Reed var. virgata, 9263, MO 1003361, Mathias, M. 645, USA, CO. (×1000)

1 4 6

2 5

7

3

Plate XII

Light micrographs of pollen grains in *Ephedra* species.
Material for examination from Dr. D. M. Jarzen
1–3. Ephedra coryi Reed var. virgata, 9263, MO 1003361, Mathias, M. 645, USA, CO. *4–7. Ephedra viridis* Coville, 9264, MO 1767696, Deaver, C. F., 5942 (×1000)

3.4. *Ephedra viridis* Coville (Plate XII, 4–7)

Spiral forms were encountered in 12.3 per cent. The polar axis is 56.0–96.0 for the typical forms; similarly to the former species the percentage distribution of pollen grains of various lengths is rather uniform. (Measuring data are based on 233 specimens.) The spiral forms are 62.0–87.0 μm long, so in this species like in the former one they are the larger specimens. The ratio of polar to equatorial axis is 1.3–3.8; ratios between 1.9 and 2.8 are found in higher percentages and 2.2 occurs most frequently (8.6%). The number of ridges generally is 7. Differences compared to the former species are the mostly undulate descent of the ridges and the coarctations at the edges of their bases. The vallae generally show a simple branching design; the relatively long (5 μm) lateral branches are 4–5 μm apart. There is no thickening at the apices of the pollen grains, the exine is 2–3 μm thick.

Discussion

(1) Similar type pollen grains of *Welwitschia* and the genus *Ephedra* can be reliably differentiated by the SEM method. On the other hand, owing to an occasional similarity occurring exclusively when the light microscope method is used, the possibility of error arises on determining the botanical relations for fossil forms. In this context we quote here some opinions: Beug (1956, p. 333): "Zusammenfassend kann man sagen daß es in der Gattung *Ephedra* der *Welwitschia* ähnliche Pollenkörner gibt und daß man diese Tatsache bei der Bestimmung fossiler Pollenkörner berücksichtigen muß". Bharadwaj (1963, p. 129/130): "It is thus apparent that the polycolpate and monocolpate condition present a difference between *Ephedra* and *Welwitschia*, of a fundamental nature, connected with the important process of their germination".

(2) Contrary to a number of publications on fossil forms the pollen grains in the genus *Welwitschia* are not characterized by any kind of thickening at the poles. Cf. Deák (1963, p. 406): "Des excellents dessins de Erdtman et de la photographie ici présentée il apparait clairement que le genre de forme *Welwitschiapites* ne peut pas être rattaché au genre *Welwitschia* actuel, comme celà a été déjà mentionné par Potonié (1958, p. 89) et Krutzsch (1961, p. 19)".

(3) The measurement variation data of pollen grains of *Welwitschia mirabilis* obtained from two different sites and exposed by different methods are highly different. In agreement with many publications we have to evaluate such data with due criticism. In this context we cite here M. van Campo (1947, p. 3): "En parcourant les articles consacrés à la question on est d'abord amené à constater que les mesures donnée pour des grains de pollen appartenant à une même espèce varient d'un auteur à l'autre". "Cernjavski a donné des exemples de courbes très différentes obtenues à partir de grains de pollen d'une même espèce récoltés en deux lieux différents." . . . "l'expérience m'a montré qu'il ne faut pas tenir compte de petites différences entre les courbes lorsqu'elles ont la même allure et la même emplacement sur le pratique."

(4) The studies on the pollen grains of the genus *Ephedra* are in the first place of supplemental character, but in certain cases of pollen dimorphism observed the difference is so great that the two type, if occurring in a fossil disperse form, would not be placed in the same form-species by any researcher (cf. *E. ochreata*, *E. americana*, *E. tweediana*).

REFERENCES

Afzelius, B. M. (1956): Electron-microscope investigations into exine stratification. *Grana Palynologica* **1:** 22–37.
Beug, H.-J. (1956): Pollendimorphismus bei Ephedra. *Naturwissenschaften* **14:** 332–333.
Bharadwaj, D. C. (1963): Pollen grains of Ephedra and Welwitschia and their probable fossil relatives. *Mem. Indian Bot. Soc.* **4:** 125–135.
Болховитина, Н. А (1963): Спорово-пыльцевая характеристика меловых отложений центральных областей СССР. *Тр. ИГН АН СССР* 145, геол. сер. **61:** 1–184.
Cookson, I. C. (1956): Pollen grains of the Ephedra type in Australian Tertiary deposits. *Nature* **7:** 47–48.
Daugherty, L. R. (1941): The Upper Triassic flora of Arizona. *Carnegie Inst. Wash.* **526:** 1–108.
Deák, H. M. (1963): Présence en Hongrie du genre Welwitschiapites Bolchovitina ex Potonié. *Grana Palynologica* **4:** 405–409.
Erdtman, G. (1965): *Pollen and Spore Morphology* (plant taxonomy Gymnospermae, Bryophyta) (text). (*An Introduction to Palynology*, III.) Almqvist and Wiksell, Stockholm.
Гладкова, А. Н., Зауер, В. В., Мчедлишвили, Н. Д. (1964): К морфологии пыльцевых зерен Ephedra. *Труды ВНИГРИ* **239:** 38–46.
Gullvag, B. (1966): The fine structure of some gymnosperm pollen walls. *Grana Palynologica* **6:** 435–475.
Hesse, M. (1984): Pollenkitt is lacking in Gnetatae: Ephedra and Welwitschia; Further proof for its restriction to the Angiosperms. *Syst. Evol.* **144:** 9–16.
Huynh, K.-L. (1974): Le problème de la polarité du pollen d'Ephedra. *Pollen et Spores* **16:** 469–474.
Jarzen, D. M. (1977): The pollen and spore reference collection at the National Museums of Canada. *Syllogeus* **13:** 1–15.
Jarzen, D. M., Whalen, G. J. (1978): Catalogue of the pollen and spore exchange collection National Museum of Natural Sciences. *Syllogeus* **16:** 1–29.
Kar, R. K. (1981): Gondiastriatites gen. nov.: a new name for the hitherto known Welwitschiapites Bolkhovitina from the Lower Gondwanas of India. *Palaeobotanist* **27:** 297–299.
Kremp, G. O. W. (1965): *Morphologic Encyclopedia of Palynology*. The University of Arizona Press: Tucson.
Krutzsch, W. (1961): Über Funde von "ephedroiden" Pollen im deutschen Tertiär. *Geologie* 10, BH **32:** 15–53.
Куваева, С. Б. (1973): О возможном растений, продуцирующих споры Corniculatisporites Kuv., со схизейными (на основании изучения морфологии спор). *Морфология и систематика ископаемых спор и пыльцы*, 18–19.
Nagy, E. (1963): Occurrence of the genus Ephedripites in the Neogene of Hungary. *Grana Palynologica* **4:** 277–280.
Planderová, E. (1976): Morphology of exine of some species of Pteridophyta and Gymnospermae pollen, examined under stereoscanning microscope. *Biol. Práce* **22:** 1–208.
Pocock, S. A. J. (1964): Pollen and spores of the Chlamydospermidae and Schizaeaceae from upper Mennville strata of the Saskatoon area of Saskatchewan. *Grana Palynologica* **5:** 129–209.
Potonié, R. (1958): Synopsis der Gattungen der Sporae dispersae II. *Beih. Geol. Jb.* **31:** 1–114.
Шахмундес, В. А. (1964): Новые виды Ephedra L. из осадков палеогена севера Западно Сибири. *Труды ВНИГРИ* **239:** 214–228.
Steeves, M. W., Barghoorn, E. S. (1959): The pollen of Ephedra. *Jour. of the Arnold Arboretum* **40:** 221–255.
Trevisan, L. (1980): Ultrastructural notes and considerations on Ephedripites, Eucommiidites and Monosulcites pollen grains from Lower Cretaceous sediments of southern Tuscany (Italy). *Pollen et Spores* **22:** 85–132.

Ueno, J. (1960): Studies on pollen grains of Gymnospermae. Concluding remarks to the relationship between Coniferae. *Journal of the Institute of Polytechnics, Osaka City University D*, **11:** 109–136.

Van Campo, M. (1947): Considérations biométriques sur les grains de pollen des Abiétinées. *Bull. Soc. Hist. Nat. Toulouse* **82:** 1–8.

Van Campo, M., Lugardon, B. (1973): Structure grenue infratectale de l'ectexine des pollens de quelques Gymnospermes et Angiospermes. *Pollen et Spores* **15:** 171–187.

Weyland, H., Krieger, G. (1953): Die Sporen und Pollen der Aachener Kreide und ihre Bedeutung für die Charakterisierung des Mittleren Senons. *Palaeontographica B*, **95:** 6–29.

Whalen, G. J., Jarzen, D. M. (1982): Catalogue of the pollen and spore exchange collection National Museums of Canada, Ottawa, Canada.

Wilson, L. R. (1959): Geological history of the Gnetales. *Oklahoma Geol. Notes* **19:** 35–40.

Wodehouse, R. P. (1935): The Pleistocene pollen of Kashmir. *Mem. Conn. Acad. Arts Sci.* **9:** 1–18.

Zhang Yu-Long, Xi Yi-Zhen (1983): Studies on the pollen morphology of Chinese Ephedra. *Acta Bot. Sinica* **25:** 418–425.

Acta Botanica Hungarica 33 (1–2), pp. 105–115 (1987)

STUDIES IN RONDELETIEAE (RUBIACEAE), IX

CINCO ESPECIES NUEVAS DEL GÉNERO *RONDELETIA* L. EN CUBA

A. BORHIDI y MAIRA FERNANDEZ ZEQUEIRA

INSTITUTO DE ECOLOGÍA Y BOTÁNICA DE LA ACADEMIA DE CIENCIAS DE HUNGRÍA,
H-2163 VÁCRÁTÓT
INSTITUTO DE BOTÁNICA DE LA ACADEMIA DE CIENCIAS DE CUBA, CIUDAD HABANA,
CALZADA DEL CERRO 1257

(Llegado: 15 Marzo 1986)

From the rich collection of the Herbarium of the National Botanical Garden of Cuba (HAJB; Habana, Calabazar) five new species were detected by the authors making a taxonomic revision of the genus *Rondeletia* for the New Flora of Cuba. Detailed descriptions of the new species are given in the paper. All the five new species were collected in the eastern provinces of Cuba. *Rondeletia arida* sp. n. is endemic of the extremely dry hilly coastal area of Baitiquiri (E. of Guantanamo). *Rondeletia bissei* sp. n. — dedicated to the memory of the excellent botanist and collector JOHANNES BISSE — is a remarkable isolated endemic of the dry montane serpentine thicket of Saca La Lengua (Sierra del Cristal). *Rondeletia bracteosa* sp. n. is a rather frequent endemic of the serpentine ranges of Moa and Baracoa, while *Rondeletia steirophylloides* sp. n. is a narrow endemic of the Mt. Pico Galán, vicarious of *R. steirophylla* Urb., endemic to Sierra del Cristal. *Rondeletia tubulosa* sp. n. is a new endemic species of the serpentine hills SE of Baracoa (Peladeros de Jauco).

Durante la preparación de una revisión taxonómica del género *Rondeletia* L. para la Nueva Flora de Cuba, los autores tuvieron oportunidad de estudiar la rica colección del Herbario del Jardin Botánico Nacional de Cuba (HAJB, Habana, Calabazar). Como primer resultado de esta revisión encontraron cinco especies nuevas para la ciencia, que se describen a continuación.

Las cinco especies fueron colectadas en las provincias orientales de Cuba. *Rondeletia arida* sp. n. es un endémico de la zona árida colinosa, cerca de las costas al Sur de Baracoa, cerca de Baitiquiri. *Rondeletia bissei* sp. n. — dedicada a la memoria de JOHANNES BISSE excelente botánico y colector de la RDA, — es un endémico aislado muy notable que vive en los matorrales montañosos áridos de la serpentina de la Loma Saca La Lengua (Sierra del Cristal). *Rondeletia bracteosa* sp. n. es una planta endémica bastante frecuente de las Cuchillas de Moa y Baracoa. En contraste, *Rondeletia steirophylloides* sp. n. es un endémico de distribución muy estrecha, en el Pico Galán y sus alrededores, donde substituye a *R. steirophylla* Urb. que es endémica de la Sierra del Cristal. *Rondeletia tubulosa* sp. n. es endémica de la zona serpentinosa de Peladeros de Jauco al SE de Baracoa.

Rondeletia arida Borhidi et Fernandez sp. nova (Figs 1, 2)

Frutex densissime ramificatus. Rami hornotini obtuse 4-anguli, pilis adpressis sursum directis puberuli, veteriores teretes, glabri, nigrescentes, longitudinaliter fissurati, laterales breves, intenodiis 2–5 mm longis ad apicem foliigeri. Stipulae late triangulares, minutae 1–1,5 mm longae, basi connatae, apice breviter mucronatae. Folia orbiculari-elliptica vel orbiculari-ovata, sessilia vel usque ad 1 mm longe petiolata, basi rotundata vel subcordata, apice rotundata et abrupte apiculata, 2–5 mm longa et 2–4 mm lata, nervo medio supra basin impresso vel omnino nullo, subtus prominulo lateralibus utroque latere 1–3 supra nullis,

Fig. 1. Holotipo de *Rondeletia arida* Borhidi et Fernandez sp. n. (HAJB 20003)

subtus prominulis et anastomosanti-reticulatis, supra strigillosa, in sicco nigra, subtus ad nervos strigilloso-hirsuta vel glabrescentia, inter nervos glabra, margine recurva vel revoluta, chartacea vel subcoriacea. Flores in axillis foliorum solitarii, bracteae 2, lineari-spathulatae vel lineari-ovatae, apice obtusae, basi stipulis interjectis in tubo brevi connatae, 1 mm longae. Calycis tubus obovatus cca 1 mm longus, strigilloso-hirsutus, lobi 4, ovati vel oblongo-ovati, apice obtusi, usque ad 1 mm longi, utrinque pilosi. Corolla non visa. Capsula glabra, 3 mm in diametro.

Holotypus: HAJB 20003; Cuba orientalis; Baitiquiri, camino a la Mina de Yeso. Col.: J. Bisse, 19. 8. 1971.

Rondeletiae apiculatae Urb. affinis a qua species nostra foliis utrinque strigilloso-hirsutis, non tomentosis, subtus postremo glabrescentibus differt.

Arbusto muy densamente ramificado. Ramitas obtusamente 4-angulosas, pubérulas con pelos adpresos, dirigidos hacía arriba; ramitas adultas cilindricas, glabras, negruzcas, longitudinalmente fisuradas, las laterales cortas, con entrenudos de 2–5 mm de largo y hojas

Fig. 2. Detaille del holótipo de *Rondeletia arida* Borhidi et Fernandez

agrupadas en el ápice de las ramas. Estípulas anchamente triangulares, muy pequeñas de 1–1,5 mm de largo, brevemente mucronadas en el ápice, connadas en la base.

Hojas orbicular-elípticas u orbicular-aovadas, sésiles o con un pecíolo de hasta 1 mm de largo, limbo de 2–5 mm de largo y 2–4 mm de ancho, redondeado y abruptamente apiculado en el ápice, redondeado o subacorazonado en la base, estrigiloso en el haz y negro cuando seco, estrigiloso-hirsuto a glabrescente en los nervios y glabro entre los nervios del envés, cartáceo o subcoriáceo, el margen recurvo o revoluto. El nervio medio hundido en la base del haz o completamente inconspicuo, prominulo en el envés; los laterales 1–3 pares nulos en el haz, prominulos y anastomosado-reticulados en el envés.

Flores solitarias en las axilas de las hojas; bracteas 2, linear-espatuladas o linear-aovadas de 1 mm de largo, obtusas en el ápice, connadas en la base con estipelas intermediarias cortas formando un tubo corto. Tubo del cáliz obovado, cca 1 mm de largo, estrigiloso-hirsuto; lóbulos 4, aovados u oblongo-aovados de hasta 1 mm de largo. Corola no vista. Cápsula globosa, glabra, de 3 mm de diámetro.

Holotipo: HAJB 20003; Cuba; Prov. Guantánamo, Baitiquirí, camino a la Mina de Yeso. Col.: J. Bisse, 19. 8. 1971. en HAJB.

Afin a *Rondeletia apiculata* Urb. de Santiago de Cuba, de la cual nuestra especie difiere en tener hojas estrigiloso-hirsutas en ambas caras, glabrescentes en el envés con la edad, no blanco-tomentosas.

Rondeletia bissei Borhidi et Fernandez sp. nova (Fig. 3)

Frutex; rami hornotini teretes, ad apicem foliigeri, pilis brevibus rigidisque retrorse strigosi et pilis suavibus tomentulosi, veteriores longitrorse striati, glabrescentes. Stipulae breviter triangulares, acutae, vix 1 mm longae, strigillosae. Folia opposita usque ad 1 mm longe petiolata, late elliptica, apice acuta et valde reflexa, basi cuneata, 4–9 mm longa et

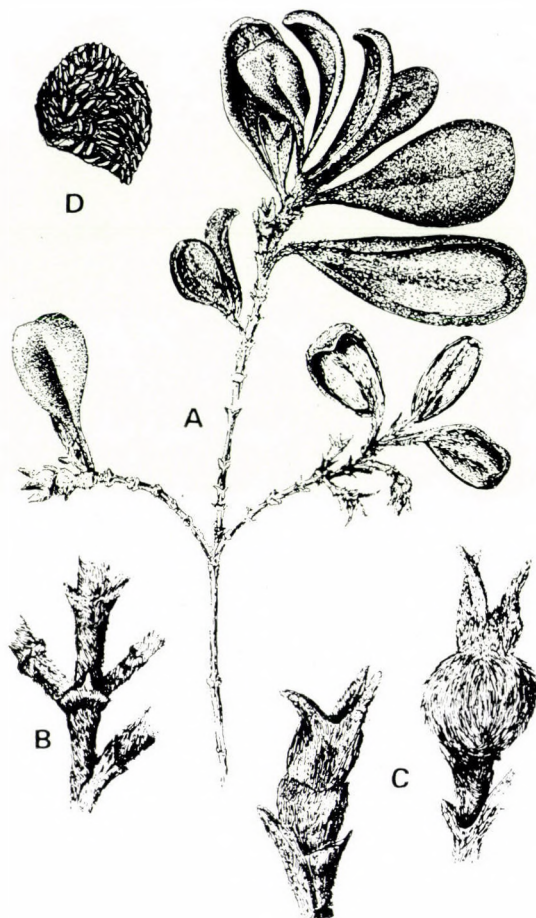



Fig. 3. Rondeletia bissei Borhidi et Fernandez sp. n.; A: rama fertil, B: ramificación con estipula, C: cáliz fructificado jóven y maduro, D: detaille de la testa de la semilla (dibujado por OCTAVIO BABILONIA a base del holótipo HAJB 30740)

2–5 mm lata, nervo medio supra inconspicuo vel impresso, subtus prominenti, basi non incrassato, lateralibus utroque latere 2, subtus inconspicuis supra nullis, lamina supra valde plicatula et glabra, subtus antrorse strigillosa ad nervos et dense albo-tomentulosa inter illos; margine anguste revoluta, rigide coriacea. Flores in axillis foliorum solitarii, sessiles vel subsessiles, pedunculis usque ad 1 mm longis, crassis. Bracteae 2, triangulares, apice acutae, 1–1,5 mm longae, basi usque 1/3–1/2 longitudinis connatae, posterior caducae. Calyx cum ovario usque ad 3 mm longus; tubus obovatus vel obtriangularis, 1–1,5 mm longus, dense retrorse strigillosus, lobi 4, triangulares, apice obtusi vel acuti, 1–1,5 mm longi, usque ad medium in tubo connati, pars libera lobi calycini 0,5–1,0 mm longa, utrinque pilosa. Corolla non visa. Capsula globosa, retrorse pilosa, 2,5–3 mm in diametro, lobis persistentibus calycinis coronata. Semina elliptica vel triangularia usque ad 1 mm longa, reticulariter areolata, exalata.

Holotypus: HAJB 30740; Prov. Santiago de Cuba; Mayari Arriba, Sierra del Cristal, Loma Saca La Lengua in fruticetis serpentinosis aridis montanis, 500 m.s.n.m. Col.: J. BISSE, M. DIAZ, L. GONZALEZ, J. GUTIERREZ, H. MANITZ; 25. 2. 1976. Isotypi: JE, B.

Obs.: *Rondeletiae plicatulae* Urb. (e Sierra de Nipe) affinis, quae a specie nostra ramulis pilis sursum directis, lobis calycinis linearibus et duplo longioribus, usque ad 4 mm longis differt. Ab omnis aliis speciebus microphyllis huius generis in Oriente septentrionali existentibus specie nostra lobis calycinis triangularibus brevibusque statim distinguenda est.

Arbusto, ramitas jóvenes cilindricas, con pelos rígidos, cortos, dirigidos hacía abajo estrigilosas y tomentulosas con pelos finos y suaves; las ramas adultas longitudinalmente estriadas y glabrescentes. Estípulas brevemente triangulares de hasta 1 mm de largo, agudas en el ápice, estrigilosas. Hojas opuestas con pecíolos de hasta 1 mm de largo, limbo anchamente elíptico, agudo y fuertemente reflejo en el ápice, cuneado en la base, 4–9 mm de largo y 2–5 mm de ancho, fuertemente plegado y glabro en el haz, estrigiloso-hirsuto en los nervios del envés con pelos rígidos dirigidos hacía el ápice, y dénsamente blanco-tomentoso entre los nervios, rígidamente coriáceo, el margen estrechamente revoluto. Nervio medio inconspicuo o hundido en el haz prominente en el envés, no engrosado en la base; los laterales 2 pares nulos en el haz, inconspicuos en el envés.

Flores solitarias en las axilas de las hojas, sentadas o subsentadas, pedunculos de hasta 1 mm de largo, gruesos. Brácteas 2, triangulares de 1–1,5 mm de largo, agudas en el ápice connadas en la base de un tercio hasta la mitad de su longitud, al fin caedizas. Cáliz con el ovario de hasta 3 mm de largo; tubo del cáliz obovado u obtriangular de 1–1,5 mm de largo densamente estrigiloso con pelos rígidos dirigidos hacia abajo; lóbulos del cáliz 4, triangulares de 1–1,5 mm de largo, obtusos o agudos en el ápice, connados en un tubo hasta la mitad, parte libre de los lóbulos de 0,5–1,0 mm de largo, pelosa en ambas caras. Corola no vista. Cápsula globosa de 2,5–3 mm de diámetro, coronada por los lóbulos del cáliz persistentes y pelosa por pelos dirigidos hacía abajo. Semillas elípticas o triangulares de hasta 1 mm de largo, reticuladas no aladas.

Holotipo: HAJB 30740; Cuba; Prov. Santiago de Cuba; Mayari Arriba, Sierra del Cristal, Loma Saca La Lengua en charrascales secos de serpentina, alt. 500 m s.n.m. Col.: J. BISSE, M. DIAZ, L. GONZALEZ, J. GUTIERREZ, H. MANITZ, 25. 2. 1976. Isotipos: JE, B.

Afin a *Rondeletia plicatula* Urb. de la Sierra de Nipe, que difiere de nuestra especie en tener ramitas pelosas con pelos dirigidos hacía el ápice, lóbulos del cáliz lineares, dos veces más largos de hasta 4 mm de largo. Nuestra especie se diferencia desde luego por sus lóbulos del cáliz cortos de todas las especies micrófilas de *Rondeletia* que existen en Norte de Oriente.

Rondeletia bracteosa Borhidi et Fernandez sp. nova (Fig. 4)

Frutex; rami hornotini compressi, non quadranguli, pilis sericeis flavescentibus obtecti, veteriores teretes, glabrescentes o glabri, striati, nigrescentes. Stipulae triangulari-ovatae, inferne et ad nervo medio dense sericei, superne purpurascenter membranaceae, glabrae inter sese usque ad medium connatae, 2–5 mm longae, saepe acutae et mucronatae. Folia 2–4 mm longe petiolata, elliptica vel obovata, basi obtusiuscula et in petiolum contracta, apice rotun-

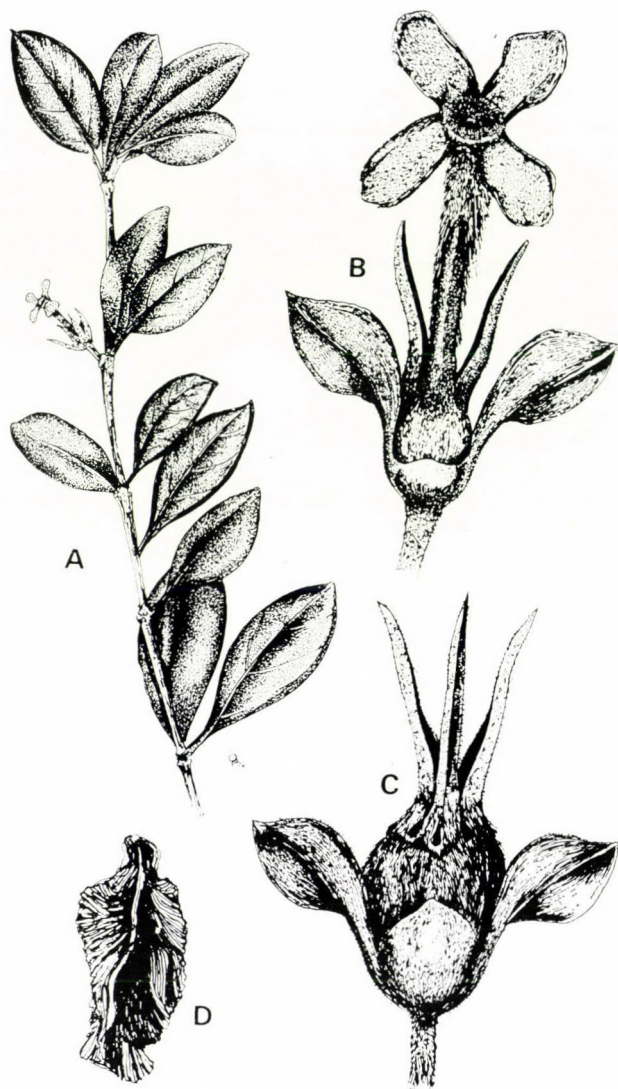



Fig. 4. Rondeletia bracteosa Borhidi et Fernandez sp. n.; A: rama florifera, B: flor, C: fruto, D: semilla (dibujo por OCTAVIO BABILONIA a base del ejemplar holótipo HAJB 42173)

data et brevissime apiculata, 1,5–2,8 cm longa et 0,4–1,8 cm lata, nervo medio supra impresso, subtus prominenti, lateralibus utroque latere 4–5, sub angulo cr. 60–80° abeuntibus, supra inconspicuis vel tenuiter impressis, subtus obsoletis vel leviter impressis, ante marginem conjunctis; lamina nigrescens in sicco, supra glabra, rugulosa, subtus glabrescens, pilis adpressis sparsis ad nervum medium, margine leviter recurva, coriacea.

Flores axillares, solitarii, 1–2 mm longe pedunculati; prophyllae foliosae, ellipticae vel lanceolatae, basi stipulis interpetiolaribus annuliformiter connatae, 5–9 mm longae, pars libera 4–6 mm longa, ab ovario liberae, in fructu anillo aperto caducae. Calycis tubus globosus, dense sericeus, limbus inferne tubuloso-connatus; lobi 4, oblongo-lineares vel lineari-subulati,

5–6 mm longi, extus glabrescentes intus puberuli, corolla 10–12 mm longa, tubus corollinus 8–10 mm longus, extus retrorse sericeus, lobi 4, rotundati, utrinque tomentulosi, 2 mm longi. Capsula globosa, pilosa, 5–7 mm in diametro, lobis calycinis persistentibus coronata. Semina numerosa, elliptica, utrinque appendicibus caudatis, forma variis, margine fimbriatis suffulta.

Holotypus: HAJB 42173; Prov. Holguin; Moa, alrededores del aserrio "La Melba" in 450–500 m. Col.: A. ALVAREZ, J. BISSE, J. GUTIERREZ, F. K. MEYER; 28. 4. 1980.

Specimina examinata: HAJB 11245. Moa, La Melba, cerca del aserrio, 500 m.s.n.m., BISSE et LIPPOLD, 27. 12. 1968. — HAJB 6273; Baracoa; subida a la Mina Iberia, entre 300 y 700 m, pluvisilva, J. BISSE et E. KÖHLER, marzo 1968. — HAJB 25676; Baracoa, Santa Maria, altiplano de la Mina Iberia, orillas del rio Iberia, 650 m alto, J. BISSE et L. GONZALEZ, apr. 1975. — HAJB 25661; Baracoa; charrascos en el valle del Rio Báez, cerca del Arroyo Naranjo, 200 m alto; J. BISSE, L. GONZALEZ, J. GUTIERREZ, apr. 1975. — HAJB 15385; Moa; La Melba, charrascales cerca del aserrio, J. BISSE, nov. 1969.

Obs.: *Rondeletiae diplocalyci* Urb. affinis, quae a specie nostra ramis hornotinis 4-angulis, stipulis 1,5–3 mm longis, foliis nervis lateralibus atroque latere 3–4 sub angulo cr. 45° abeuntibus, subtus prominentibus, chartaceis, prophyllis usque ad 3 mm longis triangulari-lanceolatis, basi cum capsula connatis, calycis lobis triangularibus, 1–2 mm longis clare distinguitur.

Arbusto con ramitas jóvenes comprimidas no 4-angulares amarillento pubérulas, ramas adultas cilindricas, estriadas, negruzcas, glabrescentes a glabras. Estípulas triangular-aovadas de 2–5 mm de largo, connadas hasta la mitad, mayormente agudas y mucronadas en el ápice, densamente sericeo pelosas en la base y sobre el nervio medio, rojizas, membranáceas y glabras arriba. Hojas con pecíolo de 2–4 mm de largo, limbo elíptico u obovado, obtusamente estrechado en el pecíolo en la base, redondeado y muy brevemente apiculado en el ápice, de 1,5–2,8 cm de largo y 0,4–1,8 cm de ancho, negro cuando seco, glabro en el haz, glabrescente en el envés con pelos esparcidos sobre el nervio medio, coriáceo. El margen ligeramente recurvo. Nervio medio hundido en el haz, prominente en el envés, los laterales 4–5 pares salen en angulo de 60–80°, inconspicuos o ligeramente hundidos en el haz, poco conspicuos o estrechamente hundidos y obscuramente anastomosados antes del margen del envés.

Flores axilares, solitarias con pedunculos de 1–2 mm de largo; prófilas foliáceas, elípticas o lanceoladas de 5–9 mm de largo, connadas con las bracteas interpeciolares en un anillo basal de 1–3 mm de ancho, parte libre de las prófilas de 4–6 mm de largo; el anillo libre, no connado con el ovario, se abre y cae en el fruto. Tubo del cáliz globoso, densamente sericeo-peloso, el limbo connado en un tubo en la base; lóbulos 4, oblongo-lineares o linear-subulados de 5–6 mm de largo, glabrescentes por fuera, pubérulos por dentro; corola de 10–12 mm de largo, el tubo de 8–10 mm de largo retrorso-sericeo por fuera, lóbulos 4, redondeados, tomentulosos en ambas caras, de hasta 2 mm de largo. Cápsula globosa, de 5–7 mm de diámetro, pelosa, coronada por los lóbulos del caliz persistentes. Semillas numerosas, elípticas, con un apendice en ambos extremos, fimbriadas en el margen.

Holotipo: HAJB 42173; Cuba; prov. Holguin; Moa, La Melba, alrededores del aserrio "La Melba" en alt. de 450–500 m. Col.: A. ALVAREZ, J. BISSE, J. GUTIERREZ, F. K. MEYER; 28. 4. 1980.

Afin a *Rondeletia diplocalyx* Urb. de la Sierra de Nipe, que difiere de nuestra especie en tener ramitas jóvenes 4-angulosas, estípulas de 1,5–3 mm de largo, hojas con nervios laterales 3–4 pares saliendo en un ángulo de cca 45°, prominentes en el envés, prófilas de hasta 3 mm de largo, triangular-lanceoladas connadas con la cápsula en la base, lóbulos del cáliz triangulares, de 1–2 mm de largo.

Rondeletia steirophylloides Borhidi et Fernandez sp. nova

Frutex; rami hornotini pilis sursum directis strigilloso-hirsuti, 4-anguli, ad apicem foliigeri, internodiis 2–10 mm longis, veteriores teretes, densissime tuberculato-rugulosi, nigrescentes. Stipulae breviter et late triangulares, 0,5–1 mm longi, apice subulatae, 1 mm longe mucronatae. Folia opposita, 1–2 mm longe petiolata, breviter orbiculari-ovata, basi rotundata vel subtruncata, obtuse attenuata apice ipso brevissime acutata et mucronulata, 5–11 mm longa et 4–7 mm lata, nervo medio ad basin versus magis superne obsolete impresso, subtus crasse et latiuscule prominente, lateralibus supra nullis, subtus utroque latere cr. 2 obsoletis vel parum prominulis, ante marginem conjunctis caeterum leviter anastomosantibus, supra glabra, in sicco transversaliter ruguloso-plicata, subtus pilis brevibus, rigidisque — ad nervos apicem versus directis — strigillosa, inter nervos pilis brevissimis tomentulosa, rigidis sime coriacea, margine non vel angustissime recurva, rariter revoluta.

Flores in axillis foliorum solitarii, sessiles vel 1–2 mm longe pedunculati; prophylla orbicularia vel orbiculari-spathulata, antice rotundata, 1–2 mm longa, superne 1–1,5 mm lata, supra glabra et nitida, basi ad pedunculus et tubum calycinum adnata, inter sese brevissime connata vel libera. Calycis lobi in floribus 4, oblongo-obovati, 2–3 mm longi, apice obtusi vel rotundati, superne paullo dilatati, cr. 1 mm lati, erecti, persistentes. Corolla verisimiliter rosea, 8–10 mm longa, tubus corollinus 6–8 mm longus, 1,5–2,2 mm latus, extus retrorse strigillosus, lobi 4, obovati, extus sericeo-hirsuti, intus suaviter tomentulosi. Capsula non visa.

Holotypus: HAJB 9495; Cuba orientalis, Prov. Guantánamo; Palenque, charrascos y pinares al suroeste de Pico Galán, 400–700 m s.n.m. Col.: J. BISSE et E. KÖHLER, mayo, 1968.

Rondeletiae steirophyllae Urb. (e Sierra del Cristal) affinis, quae a specie nostra ramis foliisque ad nervos subtus retrorse strigillosis, inter nervos dense arachnoideo-tomentosis, bracteis spathulatis 3 mm longis, tubo corollino 2–3 mm crasso, stipulis breviter apiculatis differt.

Arbusto, ramitas jóvenes 4-angulosas, con pelos ascendentes estrigiloso-hirsutas, entrenudos de 2–10 mm de largo, ramas adultas cilindricas muy densamente tuberculadas, negruzcas. Estipulas cortas, anchamente triangulares, de 0,5–1 mm de largo, subuladas en el ápice con un mucron de cca 1 mm de largo. Hojas opuestas, con pecíolo de 1–2 mm de largo, brevemente orbicular-aovadas, redondeadas a subtruncadas en la base, obtusamente estrechada hacía el ápice agudo y mucronulado, el limbo de 5–11 mm de largo y 4–7 mm de ancho, glabro y plegado en el haz, estrigiloso en los nervios del envés con pelos rígidos, dirigidos hacía el ápice, y tomentoso entre los nervios, muy rígidamente coriáceo. El margen no recurvo o muy estrechamente, raras veces revoluto. Nervio medio hundido en la base del haz, poco conspicuo hacia el ápice, ensanchado, engrosado y muy prominente en el envés; los laterales cca 2 pares, nulos en el haz, apenas prominulos u obsoletos y ligeramente anastomosados antes del margen del envés.

Flores solitarias en las axilas de las hojas, sentadas o peduculadas con pedunculos de 1–2 mm de largo. Prófilas orbiculares u orbicular-espatuladas, de 1–2 mm de largo, de 1–1,5 mm de largo, connadas con el pedunculo y con el tubo del cáliz en la base, entre si libres o muy brevemente connadas, lampiñas y brillantes en el haz, tomentosas en el envés. Lóbulos del cáliz 4, oblongo-obovados, de 2–3 mm de largo, obtusos o redondeados en el ápice, ligeramente ensanchados sobre la mitad, de cca 1 mm de ancho, erguidos y persistentes. Corola probablemente rosada, de 8–10 mm de largo, tubo de la corola de 6–8 mm de largo y 1,5–2,2 mm de ancho, retrorso-estrigiloso por fuera, lóbulos 4, obovados, sericeo-hirsutos por fuera, suavemente tomentulosa por dentro. Cápsula no vista.

Holotipo: HAJB 9495; Cuba; prov. Guantánamo; Palenque, charrascos y pinares al suroeste del Pico Galán, alt. entre 400–700 m s.n.m. Col.: J. BISSE y E. KÖHLER, mayo, 1968.

Afin a *Rondeletia steirophylla* Urb. de Sierra del Cristal, que difiere de nuestra especie en tener ramitas retrorso-estrigilosas, hojas estrigilosas en los nervios del envés por pelos dirigidos hacía la base, y aterciopeladas entre los nervios, brácteas espatuladas de hasta 3 mm de largo, estípulas brevemente apiculadas y tubo de la corola de 2–3 mm de ancho.

Rondeletia tubulosa Borhidi et Fernandez sp. nova (Figs 5, 6)

Frutex. Rami denudati, hornotini 4-anguli, flexuosi, pilis brevissimis adpressis albo-tomentosi, internodiis 2–5 mm longis, veteriores teretes, nigrescentes, longitudinaliter fissurati, ad apicem foliigeri. Stipulae triangulares, 2 mm longi, apice brevissime mucronulati. Folia elliptica vel oblongo-obovata, 2–5 mm longe petiolata, apice rotundata, basi attenuata et in petiolum protracta, 6–16 mm longa et 5–10 mm lata, nervo medio supra impresso, subtus

Fig. 5. Rondeletia tubulosa Borhidi et Fernandez sp. n.; holotipo, HAJB 39757

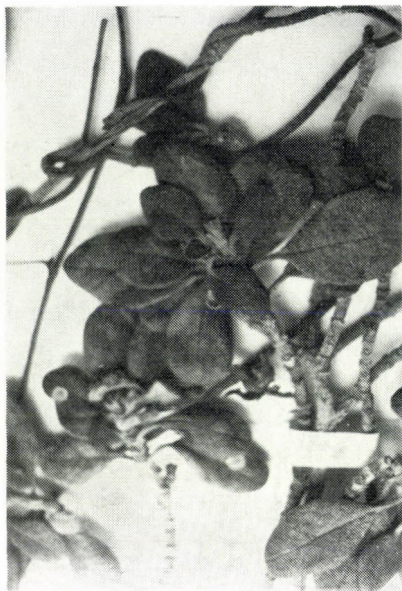



Fig. 6. Detaille del holotipo de *Rondeletia tubulosa* Borhidi et Fernandez, con flor y fruto abierto

prominente, lateralibus utroque latere 3–4, supra tenuiter impressis vel obsoletis, subtus leviter prominulis et obsolete reticulatis et anastomosantibus, supra glabra, in sicco rugulosa, plicatula, subtus pilis brevissimis homogeniter albo-tomentosa, posterior ad nervos glabrescentia, non strigillosa, margine recurva vel revoluta, coriacea.

Flores in axillis solitarii, 1–2 mm longe pedicellati vel subsessiles, pedicelli apicem versus incrassati, 1–2 mm crassi, longitudinaliter canaliculati. Bracteae triangulares, 1–2 mm longi, basi cupuliformiter connati. Calycis tubus 1,5–2,5 mm longus, superne ampliatus, connatus, superne truncatus, lobi plerumque 5 rariter 4, deltoideo-apiculati, usque ad 0,5 mm longi. Corolla 7–8 mm longa, tubus corollinus 5 mm longus, extus retrorse strigillosus, tubo calycino multo tenuior, lobi corollini obovati, 2–2,5 mm longi, extus strigilloso-pilosi, intus brevissime tomentulosi. Capsula globosa, 3 mm alta et 3–3,5 mm in diametro.

Holotypus: HAJB 39757; Cuba orientalis; Laderas al noroeste de la confluencia del Rio Baracoa con arroyos del Cayo Peladeros de Jauco. Col.: R. Berazain, R. Capote, L. Catasus, M. Duharte, A. López. 20. 2. 1979.

Rondeletiae diplocalyci Urb. (e Sierra de Nipe) affinis, a qua nostra species foliis subtus persistenter et dense albo-tomentosis, tubo calycino quasi per totam longitudinem connato, apice truncato, lobis calycinis brevissimis arcte differt.

Arbusto; ramitas jóvenes 4-angulosas, flexibles, brevemente blanco-tomentosas con entrenudos de 2–5 mm de largo, ramas adultas cilindricas, negruzcas, longitudinalmente fisuradas, hojas agrupadas en el ápice de las ramas. Estípulas triangulares de cca 2 mm de largo, brevemente mucronuladas en el ápice. Hojas elípticas u oblongo-obovadas, con pecíolos de 2–5 mm de largo, redondeadas en el ápice, atenuadas en la base y estrechadas en el pecíolo, el limbo de 6–16 mm de largo y de 5–10 mm de ancho, lampiño en el haz, y plegado cuando

seco, homogeneamente blanco-tomentoso en el envés, posteriormente glabrescente en los nervios, no estrigiloso, coriáceo. El margen recurvo o revoluto. El nervio medio hundido en el haz, prominente en el envés, los laterales 3–4 pares estrechamente hundidos u obsoletos en el haz, ligeramente prominulos y oscuramente reticulados y anastomosados en el envés.

Flores solitarias en las axilas de las hojas, subsentadas o pediceladas con pedicelos de 1–2 mm de largo engrosados hacía el ápice, de 1–2 mm de ancho, longitudinalmente canaliculados. Brácteas triangulares de 1–2 mm de largo connadas en la base en forma de cupula. Tubo del cáliz alargado de 1,5–2,5 mm de largo, ensanchado hacía arriba, brevemente denticulado o truncado en el ápice; lóbulos 5, raras veces 4, deltoideo-apiculados, de hasta 0,5 mm de largo. Corola de 7–8 mm de largo, el tubo 5 mm de largo, retrorso-estrigiloso, mucho mas delgado que el tubo del cáliz. Lóbulos obovados de 2–2,5 mm de largo, estrigiloso-pelosos por fuera, brevemente tomentulosos por dentro. Cápsula globosa, de 3 mm de alto y 3–3,5 mm de diámetro.

Holotipo: HAJB 39757; Cuba; prov. Guantánamo; laderas al noroeste de la confluencia del Rio Baracoa con arroyos del Cayo Peladeros de Jauco. Col.: R. Berazain, R. Capote, L. Catasus, M. Duharte, A. López, 20. 2. 1979.

Afin a *Rondeletia diplocalyx* Urb. de la Sierra de Nipe, de la cual nuestra especie difiere en tener hojas tomentosas en el envés con un tomento denso, blanco y persistente, el tubo del cáliz connado casi en toda su longitud, truncado en el ápice y lóbulos del cáliz muy cortos.

AGRADECIMIENTOS

El trabajo fue realizado dentro del marco del convenio bilateral firmado por las Academia de Ciencias de Cuba y la de Hungria, respectivamente. Los autores quieren expresar sus agradecimientos a Angela Leyva Sanchez, directora del Jardin Botánicas Nacional de Cuba, y a los colaboradores del HAJB, por haber facilitado el prestamo del material para el estudio taxonómico en Cuba.

REFERENCIAS

Borhidi, A. (1983): New names and new species in the flora of Cuba and Antilles, III. *Acta Bot. Hung.* **29:** 181–215.
Borhidi, A. (1985): Phytogeographic survey of Cuba, I. The phytogeographic characteristics and evolution of the flora of Cuba. *Acta Bot. Hung.* **31:** 3–34.
Borhidi, A., Fernandez, M. Z. (1982): Studies in Rondeletieae (Rubiaceae), I. A new genus: *Roigella. Acta Bot. Hung.* **27:** 309–312.
Borhidi, A., Muñiz, O. (1986): Phytogeographic survey of Cuba, II. Floristic relations and phytogeographic subdivision. *Acta Bot. Hung.* **32:** 3–48.
Fernandez, M. Z., Borhidi, A. (1985): Studies in Rondeletieae, VIII. Nuevos taxa del género *Rondeletia* en Cuba. *Acta Bot. Hung.* **31:** 147–172.
Urban, I. (1923–1928): *Symbolae Antillanae.* Vol. **9.** p .543. Berlin.
Urban, I. (1927): Plantae Haitienses et Domingenses novae vel rariores V. e cl. E. L. Ekman 1924–1927 lectae. *Ark. Bot.* **21A:** No. 5. 1–78.

Acta Botanica Hungarica 33 (1–2), pp. 117–123 (1987)

STRUCTURE, ORIGIN AND DEVELOPMENT OF THE EXTRA FLORAL NECTARIES OF *PITHECELLOBIUM DULCE* BENTH. (MIMOSACEAE)

Y. S. DAVE and A. R. S. MENON

DEPARTMENT OF BIOSCIENCES, SARDAR PATEL UNIVERSITY, VALLBH VIDYANAGAR, INDIA

(Received: 10 June 1986)

The mature nectary of *Pithecellobium dulce* is a small elongated urn-like structure situated between the insertion of each pair of pinnae and also near the apex of the petioles. The nectary has a distinct secretory zone at the tip which is covered by a cuticle. The origin of the nectary is from a group of small meristematic cells. The vascular supply to the nectary is typical in that the petiolar vascular bundles girdle at the base of the nectary before entering it and then bifurcate. It is suggested that the nectaries of *P. dulce* can be considered as a specialized EFN.

Introduction

Extra floral nectaries (EFNs) can be recognized as nectaries not directly associated with pollination (FAHN 1979). The function of EFNs has long been a matter of dispute. But the theory that they are one of plants defenses against herbivores is gaining popularity. The EFNs attract aggressive insects, such as ants, which disturb or preys upon herbivores, thereby reducing the damage to the plant (KEELER 1979). Eventhough BENTLEY (1977) in his review traced the general history of descriptions and experiments concerning the secretion of EFNs, studies pertaining to the structure, origin and development of EFNs are meagre, particularly those involving tropical species (see ELIAS 1972).

Mimosaceae is a family with EFNs of complex structures, BOUGHTON (1981), examined EFNs of 43 Australian acacias and based on their structure described three types of nectary — porate, non-porate and flat. BHATTACHARYA and MAHESWARI (1971a) distinguished three zones in the EFNs of Mimosaceae, (i) secretory zone, (ii) thick-walled zone and (iii) vascular zone. They mentioned one species of *Pithecellobium* also. ELIAS (1972) described the morphology and anatomy of the foliar nectaries of *P. macradenium* and suggested that they must be considered as anatomically highly specialized organs.

The genus *Pithecellobium dulce* is a moderately large tree armed with short straight stipular spines. The leaves are alternate and bipinnately compound. Petioles are upto 2.5 cm long. Other than the one seen adaxially between the insertion of each pair of pinnae on the rachis, a nectary may also be located near the apex of the petioles (Plate I/1).

Materials and methods

Shoot tips and mature leaflets of *P. dulce* were fixed in FAA (JOHANSEN 1940). After dehydration and infiltration 8–10 μm sections were cut. Safranin-Fast green combination and Toludine Blue were used as stains (BERLYN and MIKSCHE 1976). Nectaries were also cleared in 20% NaOH, stained with Safranin and examined for vasculature.

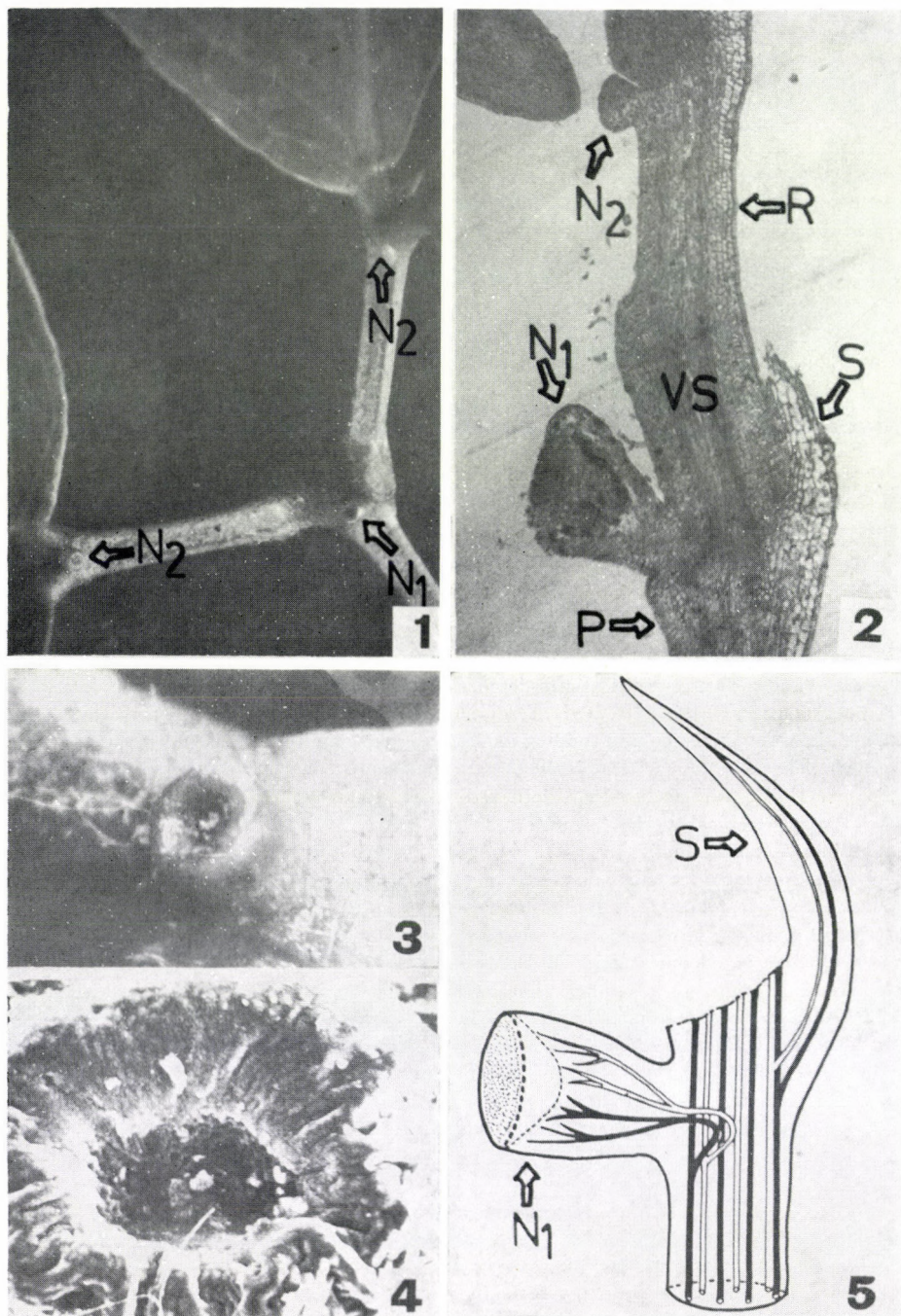



Plate I

1. Position of nectaries. ×6. — *2.* The longitudinally cut nectaries (N_1 and N_2) on the rachis. ×62. — *3.* Morphology of a nectary. (Note the distinct depression at the tip of the urn-shaped nectary.) ×60. — *4.* Scanning electron micrograph of the depression in the nectary tip. ×450. — *5.* Diagramatic representation of the vasculature. ×70

Results

The nectary on the main rachis is designated as N_1 nectary and the one which is below each pair of pinnae, i.e. on secondary rachis is denoted as N_2 nectary (Plate I/1). Plate I/2 shows both N_1 and N_2 nectaries cut longitudinally. Note that they are in two different developmental stages.

A fully matured nectary (Plate I/3) is a small urn-shaped structure with a distinct depression at the tip (non-porate type of BOUGHTON 1981). Plate I/4 gives the view of the nectary pit from the top. When the nectary is active, drop of transparent and sticky nectar oozes out from the pit. This nectar when dried on mature nectary appears brownish in colour. The nectaries seem to be more active in young leaves and almost cease secretion in very old ones.

The vascular supply to the nectary is typical. The two vascular traces from the petiolar vascular bundles girdle at the base and then enter the nectary (Plate I/5). As they enter the nectary, each bundle bifurcates into two. These branches pass through either sides of the nectary, again bifurcate and terminate at three to four cells depth beneath the secretory pit.

The structure and mode of development of the N_1 and N_2 nectaries are identical. The cells which are destined to become the nectary are first observed as a small group of densely staining meristematic cells on the rachis of the 5th or 6th node in the shoot apex (Plate II/6, 7 and 8). The N_2 meristem in figure 8 appears exactly in between two leaflets and with the rachis tissue. Plate II/7 shows the N_1 meristem on the rachis of the 9th node. This meristem has its origin from the subhypodermal cells. In the next step, periclinal divisions occur in the hypodermal layers. Plate II/9 shows a small protruded nectary in this stage. The next divisions of the nectary are both periclinal and anticlinal. Plate II/10 and 11 depict nectaries with dividing cells at different developmental stages. Note that the head cells divide periclinally, while the cells below them are anticlinally divided. The initiation of the vascular strands is first observed at this stage.

Plate II/11 is a longisection of N_1 nectary showing three different parts. At the tip region are the denser, larger and columnar cells. These epithelial cells are thickly cuticularized on their outer tangential walls. The meristematic cells just beneath, are vacuolated and dividing in two planes. The cells towards the base of the nectary are much vacuolated.

By the successive divisions of the cells of the basal region the length of the nectary increases. In a fully matured stage the nectary is an elongated urn-like structure with a slight depression at the tip. Plate III/12 to 14 show the developmental sequence of nectary which is nearing mature stage. Note the staining intensity variation of the cells of the epidermis and the secretory zone in general. These secretory cells appear to be anticlinally, periclinally and obliquely divided (Plate III/13). Thus many small cells are contributing for the nectariferous tissue.

In the mature nectary there is a thick cuticle on the tangential walls of the lateral epidermis (Plate III/14, at arrows). The epidermal cells are uneven in size also. Sometimes the cuticle is also found extending on the radial walls of the epidermis (Plate III/15, at arrows). The cuticle is thinner on the tangential walls of the epithelial cells. The presence of rhomboidal and rod shaped crystals in the central tip and outer cortex of nectary are noticeable (Plate III/16, circles). Stomata are also present on the lateral walls of nectary.

The cells of the secretory zone are full of contents (Plate III/13 and 14). The contents are also present in the pith region of nectary. The outer cortex is parenchymatous and quite often with chloroplasts (Plate III/14). The inner cortex is sclerenchymatous. There are pit canals on their lignified walls. They are transversely cut at the region below the secretory tip of the nectary. The vasculature of the nectary is connected with the ventral vascular bundles (adaxial side) of the rachis. The phloem reaches the secretory tissue at the tip of the nectary (Plate III/14).

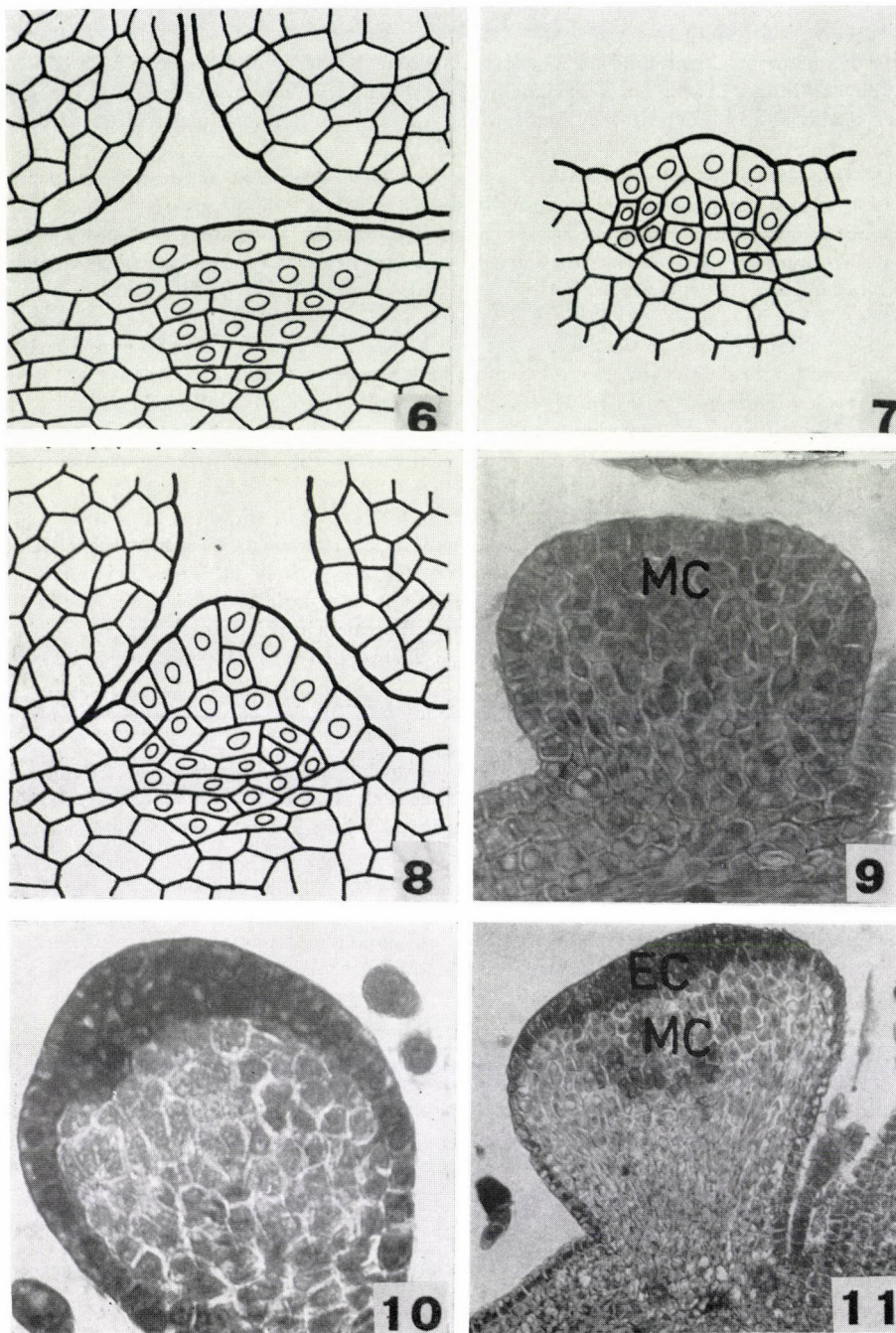



Plate II

6–8. Nectary meristems on the rachis. ×720. — *9–11.* Developing nectaries in longisections. 9. ×384, 10. ×480, 11. ×192

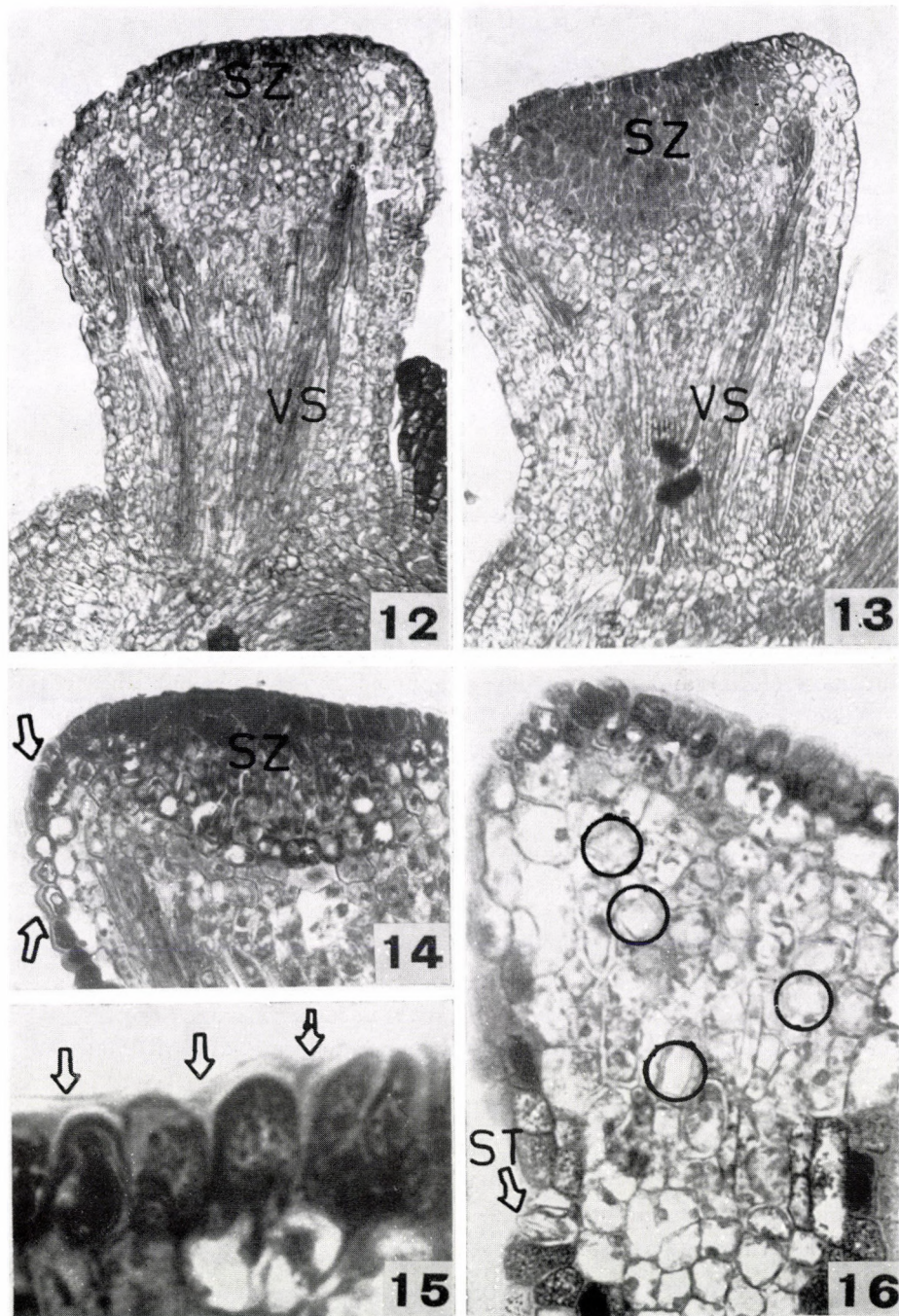



Plate III

12, 13. Nearly matured nectaries. ×180. — *14.* Secretory tip of a mature nectary. ×480. — *15.* Epidermal cells of a mature nectary showing the cuticle. ×1150. — *16.* A mature nectary with the stomata and crystals. ×450 (EC, Epithelial Cells; MC, Meristematic Cells; P, Petiole; R, Rachis; S, Stipel; ST, Stomata; SZ, Secretory Zone; VS, Vascular Supply)

Discussion

In *P. dulce*, nectary originates from a group of meristematic cells. The fact that more than one epidermal cell contributes to the formation of the nectary is noted by DAVE and PATEL (1975) in *Pedilanthus tithymaloides*. On the contrary, EFNs originating from single epidermal initial have been reported in many plants (MAHESWARI 1954, BHATTACHARYA and MAHESWARI 1971a, b). Similarly the involvement of cells belonging to the sub-epidermal layer in the development of the nectaries is in accordance with that in slipper spurge, reported by DAVE and PATEL (1975). Likewise in many plants of Mimosoideae such as *Acacia modesta* and *Dichrostachys cinerea* the nectary initials undergo anticlinal divisions. In the present observations like in *Leucaena leucocephala* (BHATTACHARYA and MAHESWARI 1971a), periclinal divisions occur.

The mature nectary of *P. dulce* is an elongated urn-like structure and its concave surface is lined by epithelial cells. The EFNs of *Pedilanthus* are observed to be long, stalked and differentiated into conical or convex head, neck and stipe. The head is covered with a secretory epithelium (DAVE and PATEL 1975). The association between calcium oxalate crystals and EFNs have been mentioned by METCALFE and CHALK (1979). This is being emphasized by BOUGHTON (1981) and again being supported by the present observation.

The vasculature to the nectary is typical in its mode of branching and finally the phloem reaches the secretory tissue at the tip of the nectary. The role of the phloem tissue in supplying the sugars to the secretory tissue of the nectary in *Ricinus communis* is well established (BAKER, HALL and THORPE 1978). As in the present observation, BOUGHTON (1981) also reported a typical type of vasculature in certain acacias.

Analysing the characters of foliar nectaries of some species of Ebenaceae, CONTRERAS and LERSTON (1984) suggested that they belong to an advenced or specialized type of nectary. The main features they selected in support of specialization are, (i) close association with vascular tissue, (ii) presence of specialized nectary sheath and subglandular parenchyma, and (iii) many small cells contributing to the nectariferous tissue, rather than fewer larger palisade-like cells. Analysing the structure of the EFNs of *P. dulce* it seems that these nectaries can also be considered as specialized. SHARMA and PILLAI (1982) also considered the EFNs of *P. dulce* to be specialized on the basis of vasculature. Likewise the 'gigas' type of EFNs of *P. macradenium* which is closely associated with vascular tissue is considered as a specialized one by ELIAS (1979).

ACKNOWLEDGEMENTS

The help rendered by Dr. K. S. Rao is gratefully acknowledged.

REFERENCES

Baker, D. A., Hall, J. L., Thorpe, J. R. (1978): A study of the extra floral nectaries of *Riccinus communis*. *New Phytol.* **81:** 129–137.
Bentley, B. L. (1977): Extra floral nectaries and protection by pugnacious body guards. *Ann. Rev. Ecol. Syst.* **8:** 407–427.
Berlyn, G. P., Miksche, J. P. (1976): *Botanical Microtechnique and Cytochemistry*. Iowa State Univ. Press, Iowa.
Bhattacharya, B., Maheswari, J. K. (1971*a*): Studies on extra floral nectaries of the leguminales, I. Papilionaceae, with a discussion on the systematics of the Leguminales. *Proc. Indian Natl. Sci. Acad.* **37:** 11–30.
Bhattacharya, B., Maheswari, J. K. (1971*b*): Studies on extra floral nectaries of the leguminales, II. The genus *Cassia* Linn. (Caesalpinaceae). *Proc. Indian Natl. Sci. Acad.* **37:** 74–90.
Boughton, V. H. (1981): Extra floral nectaries of some Australian Phyllodineous acacias. *Aust. J. Bot.* **29:** 653–664.
Contreras, L. S., Lersten, N. R. (1984): Extra floral nectaries in Ebenaceae: Anatomy, morphology and distribution. *Amer. J. Bot.* **71:** 865–872.
Dave, Y. S., Patel, N. D. (1975): A developmental study of extra floral nectaries in slipper spurge (*Pedilanthus tithymaloides*, Euphorbiaceae). *Amer. J. Bot.* **62:** 808–812.
Elias, T. S. (1972): Morphology and anatomy of the foliar nectaries of *Pithecellobium macradenium* (Leguminosae). *Bot. Gaz.* **133:** 38–42.
Fahn, A. (1979): Ultrastructure of nectaries in relation to nectar secretion. *Amer. J. Bot.* **66:** 977–985.
Johansen, D. A. (1940): *Plant Microtechnique*. McGraw-Hill, New York.
Keeler, K. H. (1979): Species with extra flora nectaries in a temporate flora (Nebraska). *The Prairie Naturalist.* **11:** 33–38.
Maheswari, J. K. (1954): The structure and development of extra floral nectaries of *Duranta plumeri* Jacq. *Phytomorphology* **4:** 208–211.
Metcalfe, C. R., Chalk, L. (1979): *Anatomy of the Dicotyledons*. Vol. **2.** Clarendon Press, Oxford.
Sharma, K. C., Pillai, A. (1982): The stem–node–leaf continuum in *Pithecellobium dulce* Benth. *Indian J. Bot.* **5:** 37–40.

Acta Botanica Hungarica 33 (1–2), pp. 125–131 (1987)

A COMPARISON OF THE GERMINATION CHARACTERS OF *DESMODIUM* SPECIES

S. C. DATTA and SONA SEN

DEPARTMENT OF BOTANY, UNIVERSITY OF CALCUTTA, CALCUTTA-19, INDIA

(Received: 30 December 1985)

Germination patterns of four species of *Desmodium* have been compared by taking into account a host of parameters. With the thickest seed coat, *D. gyrans* has the highest water uptake after 20-hr soaking. *D. gangeticum* seed, which has the thinnest coat, absorbs more water than *D. cephalotes* or *D. pulchellum*. But germination speed is greatest in *D. gyrans* and smallest in *D. cephalotes*. The hypocotyl length is maximum in *D. gyrans* and remains identical in other species. The root length is largest in *D. cephalotes* and shortest in *D. gangeticum/D. pulchellum*. In *D. gangeticum*, seed germination increases with the increasing duration of storage at 20 °C and 50 °C. For both *D. cephalotes* and *D. gyrans*, germination is reduced when exposed to the lower temperature and fails upon high-temperature exposure. *D. pulchellum* does not germinate at all upon pre-treating seeds at these two temperature extremes. In *D. cephalotes* and *D. gyrans*, increasing water stress causes a progressive decrease in germination and not imbibition. Under greater water stress, *D. gangeticum* and *D. pulchellum* show both suppressed imbibition and germination. Germination of *D. gyrans* and *D. pulchellum* is unaffected by different levels of salinity, the former having uniformly high germination values and the latter uniformly low. Thus, *Desmodium* species do not possess or require the same conditions to break seed-coat dormancy.

Introduction

The species of *Desmodium* are distributed throughout India (KANJILAL et al. 1938, GAMBLE 1957, DUTHIE 1960, HAINES 1961, COOKE 1963, PRAIN 1963). While *D. cephalotes* Wall. is found as forest undergrowth especially with Sal (*Shorea robusta* Gaertn. f.) in the north and Teak (*Tectona grandis* Linn. f.) in the south, *D. gangeticum* DC. is common in one form or the other in both waste lands and forests. *D. gyrans* DC. occurs in grasslands and as forest undergrowth too. Besides prevailing as forest undergrowth, *D. pulchellum* (Linn.) Benth. sometimes become almost gregarious. Both *D. gangeticum* and *D. gyrans* hold interest in other ways. *D. gangeticum* has been tried as green manure and cover crop in rubber and tea estates; the fibrous stems are reportedly suitable for paper making (ANON. 1952). In *D. gyrans*, the leaves are expanded somewhat horizontally during the day and droop at night; the movements are such that the apex of each of the two basal leaflets executes through an ellipse and are induced by changes in turgidity of the pulvinus of the petiole of the leaflets (STILES–COCKING 1969).

Reproduction by seed in *Desmodium* species (as well as in other legumes) in the tropical-vegetation zones has been studied among others by MISRA (1967), BHAT (1968), TRIPATHI–SHRIVASTAVA (1970), DATTA–SINHAROY (1975) and SEN (1977). In these studies, the central problem is the poor germination of the seed as it is secured from the parent plant. It is not known whether the seeds lost their germinability or whether they required special conditions to arouse germination. In general, seeds of leguminous plants are considered to possess coat-imposed dormancy. This physical barrier may cause the seed to lie dormant for many years

unless some form of treatment is carried out to improve permeability. Germination physiology of *Desmodium pulchellum* has been subjected to a preliminary investigation only (TRIPATHI–SHRIVASTAVA 1970). No data were available in the literature on the germination behaviour of *Desmodium* species native to eastern India. The purpose of this paper is to provide such information for four *Desmodium* species. The present work also compares the germination of *D. gyrans*, a species regarded to exemplify the so called variation movements of leaflets (STILES–COCKING 1969), with that of other species devoid of this kind of autonomic movements. Such comparisons have been made on the basis of their seed-coat thickness, water uptake, germination speed, root length and hypocotyl length as well as the influence of dry storage at two temperatures, water stress and salinity to relieve seed dormancy.

Material and methods

One batch of fresh seeds of each species was obtained from the Deputy Director, Indian Botanic Gardens, Howrah, West Bengal and used for all of the experiments described.

Seeds were pre-treated by storing them dry in stoppered glass vials at low (20 °C) and high (50 °C) temperatures. The duration of pre-treatments was 1–4 weeks. Such seeds were scattered to imbibe and germinate at the fluctuating room temperature (24–29 °C).

Before the seeds were soaked in water, they were dry-heated at 70 °C for 4 hr. After soaking, their weights were recorded at regular intervals. As soon as the seeds started swelling, transverse sections were cut from the middle portion of a few seeds of each species. These sections were mounted in water and the thickness of entire seed coat measured by means of ocular micrometer.

Seeds, pre-heated at 70 °C for 4 hr, were plated onto Petri-dishes (7 cm diam) where water supply was regulated by keeping on 1 (for no stress), 2 (slight stress) and 4 (moderate stress) circles of filter paper and adding the same quantity of water (2 ml per dish). After treatment at 70 °C, some of the seeds were held at varying levels of salinity (created by 0.0125–0.2 *M* NaCl).

At each temperature set and for each species, 4 replicates of 10 seeds were kept. Seeds with nearly 1 mm radicle were chosen as germinated. Number of these seeds were scored at 24-hr intervals. The speed of germination index was calculated according to the formula given by CARLEY—WATSON (1968).

Results

(a) *Thickness of seed-coat:* From the measurements of seed-coat thickness, it appears that *D. gyrans* had the thickest coat (0.206 mm) and *D. gangeticum* the thinnest (0.083 mm). The seeds of *D. cephalotes* (0.143 mm) and *D. pulchellum* (0.142 mm) produced coats of the same thickness, being higher than *D. gangeticum* and lower than *D. gyrans.*

(b) *Uptake of water:* Except *D. pulchellum*, seeds of no other species imbibed water after 1 hr of soaking (Table 1). At the end of the 2-hr period, water uptake of both *D. cephalotes* and *D. gangeticum* was the same. However, these values were higher than those of *D. gyrans* and *D. pulchellum.* After 4-hr and 8-hr soaking, *D. gangeticum* still maintained a higher water absorption as compared to seeds of other species. After 20-hr soaking, *D. gyrans* took the lead and was far ahead of seeds of other species. Finally, *D. gangeticum* absorbed more water than either *D. cephalotes* or *D. pulchellum.*

(c) *Germination traits:* The germination speed was highest in *D. gyrans* and lowest in *D. cephalotes*, while *D. gangeticum* was intermediate in position (Table 2). As seeds of *D. pulchellum* failed to germinate after 5 days, its germination speed was nil.

While maximum germination in *D. pulchellum* was attained in 11 days, the time period was 8 days for both *D. cephalotes* and *D. gyrans* as well as 6 days for *D. gangeticum* (Table 2).

Table 1

Percentage of water uptake when ungerminated seeds of Desmodium *were held at room temperature*

Species	Percentage of water uptake				
	1 hr	2 hr	4 hr	8 hr	20 hr
D. cephalotes	0	4.68	8.07	8.25	20.65
D. gangeticum	0	4.16	25.70	34.39	35.10
D. gyrans	0	1.18	7.44	31.17	73.65
D. pulchellum	0.62	0.64	4.82	10.53	11.77

Table 2

Germination traits of Desmodium *after being pretreated at 70° C for 4 hr and then transferred to room temperature*

Species	Speed of germination index	Percentage of germination	Root length* (cm)	Hypocotyl length* (cm)
D. cephalotes	1110	77.5 ± 16.0	2.78 ± 0.29	1.86 ± 0.09
D. gangeticum	2370	80.0 ± 7.0	0.63 ± 0.21	1.63 ± 0.08
D. gyrans	3050	90.0 ± 0.1	1.74 ± 0.58	3.46 ± 0.15
D. pulchellum	0	40.0 ± 5.7	0.82 ± 1.08	1.36 ± 0.11

* Based on 5-day old seedlings

The hypocotyl length was greatest in *D. gyrans* (Table 2). In other species, the hypocotyl remained more or less the same. As regards the root length, it was highest in *D. cephalotes* and this was followed by *D. gyrans.* The root was of the same length in *D. gangeticum* and *D. pulchellum*, both showing poor growth in comparison with *D. cephalotes* and *D. gyrans.*

(d) *Dry storage:* While *D. pulchellum* failed to imbibe by storing at 20 °C, they imbibed completely at 50 °C (Table 3). Such complete imbibition was achieved by both *D. cephalotes* and *D. gyrans* upon pre-treating seeds at 50 °C. Imbibition decreased with increasing duration of pre-treatment at 20 °C for *D. cephalotes*, but increased with increasing duration for *D. gangeticum.* With *D. gyrans*, increasing duration of pre-treatment at 20 °C resulted in little or no increase in imbibition.

No seeds of *D. pulchellum* germinated regardless of the low- or high-temperature pretreatment and the duration (Table 3). For *D. cephalotes* germination was reduced with increasing duration at 20 °C and no germination occurred when seeds were stored at 50 °C. With *D. gangeticum*, germination increased progressively with increasing duration of 20 °C and gradually with increasing duration of 50 °C. Whereas *D. gyrans* germinated poorly when exposed to 20 °C, they did not germinate at all upon 50 °C-exposure.

Compared to *D. gangeticum*, *D. cephalotes* gave higher imbibition and germination on being kept at 20 °C for 1 week. However, *D. gangeticum*, yielding low imbibition and germination percentages 20 °C for 1–4 weeks, improved both the processes upon exposure to 50 °C. Both *D. gangeticum* and *D. gyrans* exhibited poor imbibition and germination for seeds which were stored dry at 20 °C.

Table 3

Effect of dry storage of Desmodium *seeds at low (20 °C) and high temperature (50 °C) upon subsequent imbibition and germination at room temperature*

Species	Duration of storage (weeks)	Dry storage at 20 °C: Percentage of imbibition	Dry storage at 20 °C: Percentage of germination	Dry storage at 50 °C: Percentage of imbibition	Dry storage at 50 °C: Percentage of germination
D. cephalotes	1	82.5 ± 7.4	82.5 ± 7.4	100.0 ± 0	0
	2	72.5 ± 9.6	72.5 ± 9.6	100.0 ± 0	0
	4	62.5 ± 7.4	50.0 ± 8.6	100.0 ± 0	0
D. gangeticum	1	17.5 ± 6.4	10.0 ± 3.5	55.0 ± 8.2	40.0 ± 10.6
	2	22.5 ± 5.4	22.5 ± 5.4	95.0 ± 4.3	92.5 ± 8.4
	4	30.0 ± 8.6	30.0 ± 8.6	72.5 ± 18.1	67.5 ± 13.8
D. gyrans	1	25.0 ± 4.3	22.5 ± 5.4	100.0 ± 0	0
	2	30.0 ± 6.1	22.5 ± 8.2	100.0 ± 0	0
	4	25.0 ± 9.0	12.5 ± 8.2	100.0 ± 0	0
D. pulchellum	1	0	0	100.0 ± 0	0
	2	0	0	100.0 ± 0	0
	4	0	0	100.0 ± 0	0

(e) *Water stress:* In *D. cephalotes*, increasing water stress was accompanied by a progressive decrease in germination and not imbibition which was complete under all conditions (Table 4). Both imbibition and germination values were lowered with increases in water stress in *D. gangeticum* and *D. gyrans*. Compared to other species, *D. pulchellum* imbibed and germinated poorly.

Table 4

Effect of water stress on the imbibition and germination percentages of Desmodium *after being pre-treated at 70 °C for 4 hr and then transferred to room temperature*

Species	Water stress (with circles of filter paper)	Percentage of imbibition	Percentage of germination
D. cephalotes	1	100.0 ± 0	77.5 ± 8.5
	2	100.0 ± 0	72.5 ± 7.5
	4	97.5 ± 2.2	70.0 ± 4.0
D. gangeticum	1	100.0 ± 0	92.0 ± 6.5
	2	75.0 ± 7.5	50.0 ± 20.3
	4	62.2 ± 18.5	55.0 ± 5.6
D. gyrans	1	100.0 ± 0	97.5 ± 0.87
	2	100.0 ± 0	85.0 ± 0.27
	4	100.0 ± 0	75.0 ± 0.17
D. pulchellum	1	22.5 ± 9.2	12.5 ± 6.4
	2	22.5 ± 7.3	7.5 ± 4.1
	4	18.5 ± 4.1	5.0 ± 2.5

(f) *Salinity:* While there was imbibition under all levels of salinity and for all species, this was very low for *D. pulchellum* (Table 5). Furthermore, germination was reduced with increasing salinity in both *D. cephalotes* and *D. gangeticum*. However, germination of *D. gyrans* was unaffected by salinity; the same was the situation with *D. pulchellum* which had the usual poor germination.

Table 5

Effect of salinity on the imbibition and germination percentages of Desmodium *after being pre-treated at 70 °C for 4 hr and then transferred to room temperature*

Species	Levels of salinity (*M* NaCl)	Percentage of imbibition	Percentage of germination
D. cephalotes	0.0125	100.0 ± 0	85.0 ± 15.1
	0.025	100.0 ± 0	100.0 ± 0
	0.05	100.0 ± 0	100.0 ± 0
	0.1	100.0 ± 0	50.0 ± 10.0
	0.2	100.0 ± 0	0
D. gangeticum	0.0125	97.5 ± 2.2	72.5 ± 8.9
	0.025	90.0 ± 6.1	72.5 ± 7.4
	0.05	95.0 ± 4.3	50.0 ± 13.7
	0.1	100.0 ± 0	62.5 ± 16.7
	0.2	100.0 ± 0	37.5 ± 20.7
D. gyrans	0.0125	100.0 ± 0	85.0 ± 2.5
	0.025	100.0 ± 0	80.0 ± 3.5
	0.05	100.0 ± 0	90.0 ± 3.5
	0.1	100.0 ± 0	90.0 ± 3.5
	0.2	97.5 ± 2.2	82.5 ± 5.4
D. pulchellum	0.0125	57.5 ± 8.2	37.5 ± 6.5
	0.025	42.5 ± 9.9	35.0 ± 8.3
	0.05	47.5 ± 6.5	42.5 ± 5.4
	0.1	47.5 ± 8.9	42.5 ± 7.4
	0.2	55.0 ± 14.2	45.0 ± 8.2

Discussion

All the four species do not contain the same hereditary property and the depth of seed dormancy. Though the seed coat of *Desmodium gyrans* is the thickest, it does not follow that it will have the lowest water uptake. In fact, this species has the highest water uptake. *D. gangeticum*, endowed with the thinnest seed coat, absorbs more water than either *D. cephalotes* or *D. pulchellum* whose seed coat is less thicker than *D. gyrans*. Such water uptake and seed-coat thickness of these species are not necessarily reflected in their germination responses subsequently.

Differences are striking amongst the species of *Desmodium* both in terms of the water uptake as well as the speed of germination index or maximum germination. Seeds of those species which have the capacity to take up more

water have also the same ability to germinate to a considerable extent. Whereas *D. pulchellum* has the minimum water uptake and *D. gyrans* the maximum, the minima and maxima for germination speed and highest germination are shared by these two species. In this connection, *D. gangeticum* takes the lead before *D. cephalotes* and lags behind *D. gyrans*. Compared to *D. gangeticum*, the germination of *D. pulchellum* seeds is slower and delayed. However, both *D. cephalotes* and *D. gyrans* germinate earlier than *D. pulchellum* and later than *D. gangeticum*. Germination percentages may be adopted as a close approximation to the potential germination of a species and forms a useful figure for comparison when assessing the effect of other treatments.

Coupled with the poorest germination of *D. pulchellum* is the fact that it has the lowest hypocotyl length. However, its root length is greater than that of *D. gangeticum* and smaller than that of either *D. cephalotes* or *D. gyrans*. The seeds of *D. gyrans*, which has maximum germination, shows the most luxuriant hypocotyl growth. While *D. gangeticum* germinates better than *D. cephalotes*, the hypocotyl length of the former is less than that of the latter. The success of germination in a species can be ensured by proper growth of the root and hypocotyl. In this respest, *D. gyrans* is ostensibly most successful and *D. pulchellum* poorest of the lot.

It is interesting to consider the impact of storage temperatures on subsequent imbibition and germination. *D. pulchellum* is sensitive to both low and high temperatures, for there is only imbibition upon pre-treatment at 50 °C but no germination after pre-treating the seeds at his temperature or 20 °C. While *D. gyrans* shares with *D. pulchellum* and *D. cephalotes* the complete imbibition of seeds upon exposure to the higher temperature, there is both poor imbibition and germination of *D. gyrans* following the dry storage of the seeds at 20 °C. Though imbibition and germination decreases with increasing duration of pre-treatment at 20 °C for *D. cephalotes*, the reverse is true for *D. gangeticum*. Moreover, the seeds of *D. gangeticum* react most favourably to high-temperature stimulus, which not only enhances imbibition but also proves helpful in increasing the germinability. Hence, the effects of temperature pre-treatments in overcoming seedcoat impermeability in *Desmodium* species are noteworthy.

In the matter of the effect of water stress on pre-heated (70 °C) seeds, the four species of *Desmodium* can be separated into two groups. In one group, which includes *D. cephalotes* and *D. gyrans*, increasing water stress causes a progressive decrease in germination and not imbibition. The other group, to which *D. gangeticum* and *D. pulchellum* belong, indicates reduced imbibition and germination with greater water stress. The response of seeds to high-temperature pre-treatment and water-stress post-treatment is somewhat uniform despite the fact that the seed coat is of variable thickness in all four species.

Similar to water-stress, the germination of *Desmodium* species is affected by salinity. As the levels of salinity are increased, imbibition does not decline to the same extent as germination in *D. cephalotes* and *D. gangeticum*. While poor germination is the salient feature of *D. pulchellum* seeds, the germination of *D. gyrans* is not at all affected by greater salinity. Perhaps the structural form of *D. gyrans* seeds is such that it can tolerate not only the impact of the high-temperature pre-treatment but also the high salinity post-treatment.

According to Thompson (1970), the germination response of seeds may be correlated with the area of origin and the geographical range of the species. Though all four species of *Desmodium* originate from a common tropical habitat, their germination characters differ from one species to another and most of them do not have the same requirement as *D. gyrans* to alleviate seed dormancy. These differences, in the opinion of Vegis (1963), probably correspond to their plasticity at least during their initial establishment in conjunction with the ecophysiological requirements.

REFERENCES

Anonymous (1952): *The Wealth of India. Raw Materials* **3**, 41. Council of Scientific & Industrial Research, New Delhi.

Bhat, J. L. (1968): Seed coat dormancy in *Indigofera glandulosa*. *Trop. Ecol.* **9:** 42–51.

Carley, H. L., Watson, R. D. (1968): Effect of various aqueous plant extracts upon seed germination. *Botan. Gaz.* **129:** 57–62.

Cooke, T. (1963): *Flora of Bombay* (Reprinted edn.) **1**, 376–382. Botanical Survey of India, Calcutta.

Datta, S. C., Sinharoy, S. P. (1975): Germination-regulating mechanisms in aquatic angiosperms. *Brotéria* **44:** 81–91.

Duthie, J. F. (1960): *Flora of the Upper Gangetic Plains.* (Reprinted edn.) **1:** 264–288. Botanical Survey of India, Calcutta.

Gamble, J. S. (1957): *Flora of the Presidency of Madras.* (Reprinted edn.) **1:** 242–245. Botanical Survey of India, Calcutta.

Haines, H. H. (1961): *The Botany of Behar and Orissa.* (Reprinted edn.) **2:** 273–278. Botanical Survey of India, Calcutta.

Kanjilal, U. N., Das, A., Kanjilal, P. C., De, R. N. (1938): *Flora of Assam.* **2:** 47–59. Govt. of Assam Publ., Shillong.

Misra, R. (1967): Ecological studies of some weeds of Upper Gangetic Plains. *P. L.* 480 *Research Project* **2:** 106–114.

Prain, D. (1963): *Bengal Plants.* (Reprinted edn.) **1:** 303–305. Botanical Survey of India, Calcutta.

Sen, D. N. (1977): *Environment and Seed Germination of Indian Plants.* Chronica Botanica Co., New Delhi.

Stiles, W., Cocking, E. C. (1969): *An Introduction to the Principles of Plant Physiology.* 3rd edn. Methuen & Co., London.

Thompson, P. A. (1970): Characterisation of germination to temperature of species and ecotypes. *Nature* **225:** 827–831.

Tripathi, R. S., Shrivastava, P. P. (1970): Preliminary studies on germination behaviour of *Desmodium pulchellum* (Linn.) Benth. *Trop. Ecol.* **11:** 75–79.

Vegis, A. (1963): Climatic control of germination, bud break and dormancy. In: *Environmental Control of Plant Growth.* L. Evans (ed.), Academic Press, New York & London.

Acta Botanica Hungarica 33 (1–2), pp. 133–138 (1987)

CASE STUDY ON TUMOR-LIKE FORMATION ON THE LEAVES OF SUNFLOWER (*HELIANTHUS ANNUUS* L.)

F. HERDI

MERIKLON RES. LABS CO., 1028 BUDAPEST, PATAKHEGYI ÚT 83.

(Received: 1 February 1986)

An effect of dicamba (3,6-dichloro-o-anisic acid) manifesting itself in tumor-like formations was observed on the leaves of sunflower. Light microscopic examination of such leaves revealed a substantial structural difference as compared to controls. The leaf blade was thicker and large-sized vascular bundles were found between the palisade and spongy parenchyma cell-layers. In some areas the spongy parenchyma cells appeared similar to the palisade parenchyma cells. Palisade and spongy parenchyma cells could not be found in the tumor-like part of the leaf, which was almost completely lignified and filled with numerous tracheids mainly in radial arrangement.

Introduction

Hormone type herbicides can cause a variety of external and internal changes in both plants and animals, however changes were found also for humans. Plant organs growing both in the soil and aboveground can be severely affected by hormone type herbicides especially in dicotyledonous plants.

In the sunflower, the thickness of the leaf responded differently to the effects of 2,4-D MCPA and dicamba (HERDI 1981, 1983*a*, 1983*b*). HACCIUS and SCHNEIDER (1958) (loc. cit. KIERMAYER 1964) observed deformation of the spongy parenchyma cells due to application of 2,4-D. The vascular bundles were placed close to one another in the leaves due to the treatment of 2,4-D and other growth-regulating substances (EAMES 1949, WATSON 1948). Veins protruded considerably on the lower side of the bean leaves due to the treatment of 2,4-D (FELBER 1948, WATSON 1948) and of the sunflower leaves due to the treatment of dicamba and MCPA (HERDI 1981, 1983*a*). MEYER (1970) noticed xylem and phloem damage in the stem and root due to the effect of picloram and 2,4,5-T. EAMES (1949) found abnormal development and lengthening of the vascular bundles of the leaf. HERDI (1979, 1982, 1983*c*, 1983*d*) found deformation and multiplication of vascular bundles in case of exposure to 2,4-D MCPA and dicamba.

Studies on mice exposed to 2,4,5-T showed increased tumor incidence (MURÁNYI-KOVÁCS et al. 1976, loc. cit. HARDELL and SANDSTRÖM 1979). AXELSON et al. (1974) (loc. cit. AXELSON et al. 1980) found increased overall tumor morbidity among railroad workers exposed to the herbicides amitrol, 2,4-D and 2,4,5-T.

Material and method

Sunflower plants (*Helianthus annuus* L. cv. VNIIMK 6541) were used. Seeds were sow on May 12th and the treatments made at the two-leaved vegetation stage of the plants, on June 12th. Plants were sprayed with an aqueous 1000 ppm dicamba solution (3,6-dichloro-o-anisic acid) technical grade. Leaf samples were collected from treated and untreated control plants and were fixed in 40% alcohol on July 11th, when the plants were at the 17-leaved stage. Sections were made from the leaf using an MC-2 sliding microtome with a KTOC-2 electric freezing equipment. Staining was made with safranine and Ehrlich's acidic hematoxylin.

Results

Control leaves were bifacial (Fig. 1) with stomata in both the upper and lower epidermis. The palisade parenchyma layer consisted of 2 rows of elongated cells loosely spaced arranged perpendicular to the epidermis. The cells of the spongy parenchyma layer were 2–3 rows thick. The leaf blade was of uniform

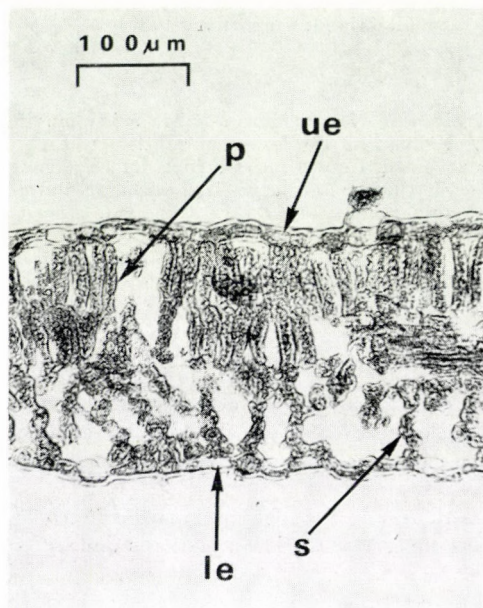



Fig. 1. Cross-section of the leaf of the untreated control plant. p = palisade parenchyma cells, s = spongy parenchyma cells, ue = upper epidermis, le = lower epidermis

thickness, and there were no protrusions or indentions either from the upper or the lower epidermis.

Treatment with dicamba resulted in tumor-like formations on various portions of the leaf. The tumor-like formations spread over both sides of the leaf.

The treated leaf blades were of uneven thickness, and considerably thicker overall than that of the controls. The protrusions and indentions were insignificant on the upper epidermis, but quite noticeable on the lower epidermis. The veins of the treated leaves protrude considerably on the lower side. The vascular bundles take up 1/3 part of the leaf thickness at this point. Multicellular hairs on the lower vein surface occur close together in loose groups, contrary to that of the controls. The palisade parenchyma consisted of 1–3 cell rows in those parts of the leaf blade, where no tumor-like formations occurred (Fig. 2). These cells were fitted tightly together unlike these of

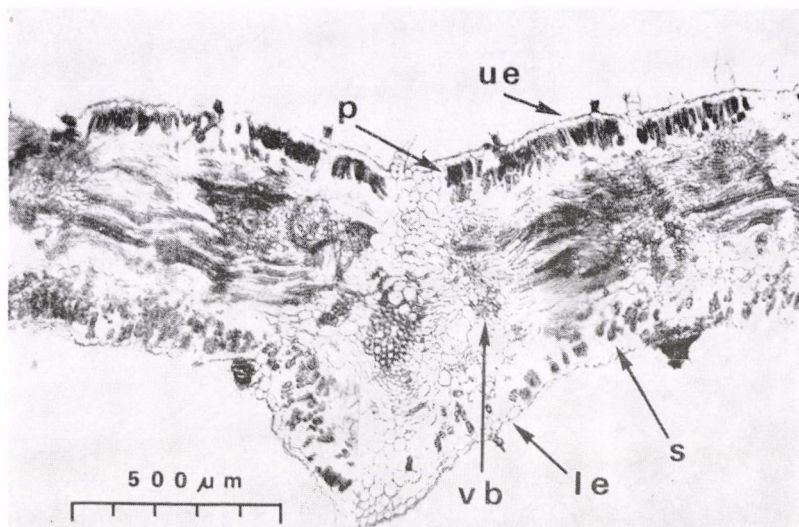



Fig. 2. Cross-section of the leaf of the plant treated with 1000 ppm dicamba. p = palisade parenchyma cells, s = spongy parenchyma cells, ue = upper epidermis, le = lower epidermis, vb = vascular bundles

the controls. The spongy parenchyma cells in these some areas were in 1–3 rows, and in some places they were larger than normal.

The cellular organization of the leaf close to the "tumors" (Fig. 3a) was to some extent similar to that of the controls inasmuch as a row of palisade parenchyma definitely occurs below the upper epidermis. The tissue region corresponding to the spongy parenchyma is however greatly enlarged decounting for the increased thickness of the leaf at this point. Enlarged cells and vascular bundles were found between the palisade and spongy parenchyma layers. Xylem elements occurred in large quantity in these vascular bundles. Palisade and spongy parenchyma cells were absent in the area next to the tumor-like formations. Below the epidermis there were large-sized parenchyma cells.

The tumor-like formation (Figs 3a and 3b) were almost completely lignified, parenchyma cells occurring only in some isolated regions. Tracheids found in the tumor-like formation in large numbers were often arranged in radial direction.

Discussion

These results show that dicamba causes serious alteration in the leaf tissue of sunflower similarly to the effect of phenoxyacetic acids.

In the treated leaf of sunflower there were large-sized cells between the palisade and parenchyma cells. ALLARD et al. (1946) found cell proliferation

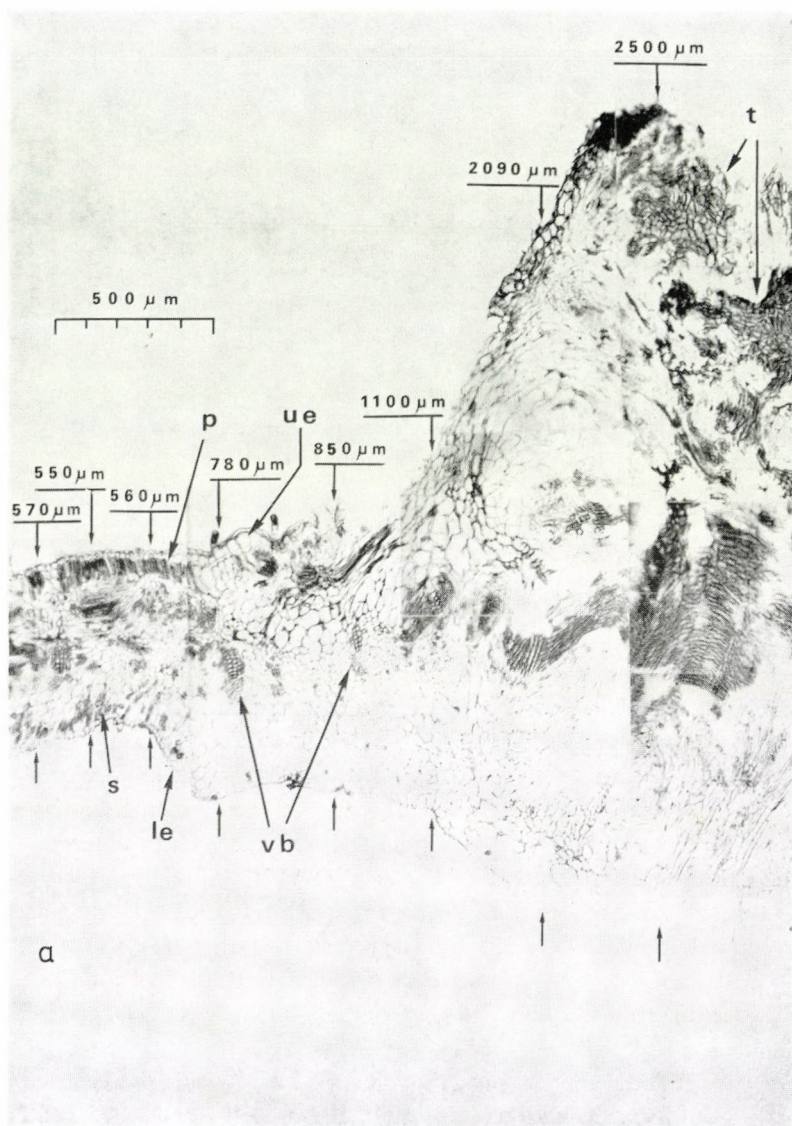



Fig. 3a. Cross-section of the leaf of the plant treated with 1000 ppm dicamba, with a part of the tumor-like formation. Leaf thickness data are marked. p = palisade parenchyma cells, s = spongy parenchyma cells, ue = upper epidermis, le = lower epidermis, t = tracheid, vb = vascular bundle

and enlargement for beans as a result of exposure to 2,4-D. FELBER (1948) and TUKEY et al. (1945) noticed cell expansion and cell division due to the effect of 2,4-D. PIZZOLATO and REGEHR (1981) observed hypertrophy, hyperplasia and plastid destruction for tomatoes exposed to 2,4-D. Tumor-like

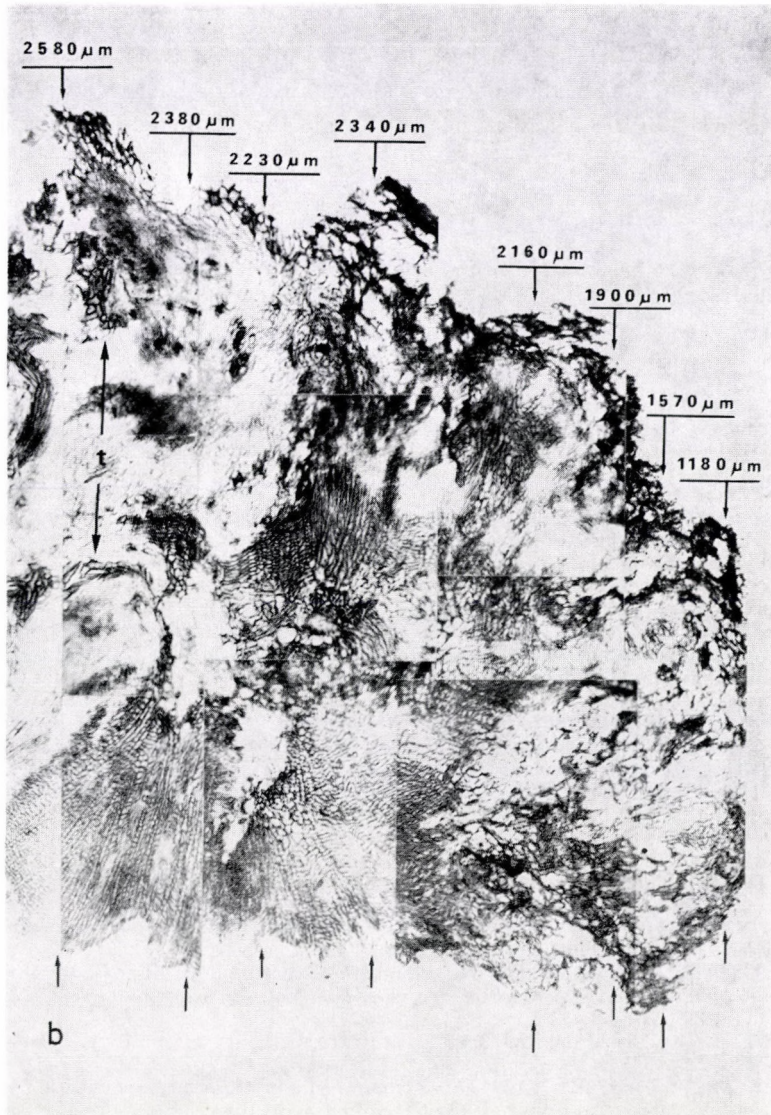



Fig. 3b. Cross-section of the greater part of the tumorlike formation

formations developed on the leaf. MURRAY and WHITING (1947) found cell proliferation and tumor development for beans as a result of exposure to 2,4-DB. According to SACH's experiment (1975) the tumor developed due to the effect of auxins and cytokinines has a similar structure to that of the tumor caused by *Agrobacterium tumefaciens*; ARLT and FEYERABEND (1973) observed similar results in the case of the hormone type herbicides. In the tumor-like formation, tracheids can be found in large numbers. FROHBERG

(1951) (loc. cit. KIERMAYER 1964) found cell proliferation due to the effect of 2,4-D immediately below the point of application and observed that cells deriving from such meristematic zones turn into tracheids. SOROKIN et al. (1962) found hyperplasia and imperfect xylem development for peas exposed to 2,4-D and IAA.

REFERENCES

Allard, R. W., Robert de Rose, H., Swanson, C. P. (1946): Some effects of plant growth-regulators on seed germination and seedling development. *Bot. Gaz.* **107:** 575–583.

Arlt, K., Feyerabend, G. (1973): *Herbizide und Kulturpflanzen.* Akademie-Verlag, Berlin.

Axelson, O., Sundell, L., Andersson, K., Edling, C., Hogstedt, C., Kling, H. (1980): Herbicide exposure and tumour mortality. *Scand. J. Work Environ. Health* **6:** 73–79.

Eames, A. J. (1949): Comparative effects of spray treatments with growth-regulating substances on the nut grass, Cyperus rotundus L., and anatomical modifications following treatments with butyl 2,4-dichlorophenoxyacetate. *Amer. J. Bot.* **36:** 571–584.

Felber, I. M. (1948): The formation of protuberances on bean leaves in response to 2,4-D treatments. *Amer. J. Bot.* **35:** 555–558.

Hardell, L., Sandström, A. (1979): Case-control study: soft tissue sarcomas and exposure to phenoxyacetic acids or chlorophenols. *Br. J. Cancer* **39:** 711–717.

Herdi, F. (1979): The dicamba-induced damage in the petiole of the beetroot (Beta vulgaris L. convar. conditiva Alef.). *Acta Phytop. Acad. Sci. Hung.* **14:** 409–417.

Herdi, F. (1981): Szöveti elváltozások dicamba hatására a napraforgó (*Helianthus annuus* L.) lomblevelében [Tissue alterations due to dicamba in the foliage leaf of sunflower (*Helianthus annuus* L.)]. (Hungarian with English abstract. *Növénytermelés* **30:** 229–239.

Herdi, F. (1982): Dicamba hatása a napraforgó (*Helianthus annuus* L.) levélnyelében levő szállítónyalábokra [Effect of dicamba on the vascular bundles of sunflower (*Helianthus annuus* L.) leaf petioles]. (Hungarian with English, German and Russian abstracts. *Növényvédelem* **XVIII:** 302–312.

Herdi, F. (1983*a*): MCPA induced tissue changes in sunflower (*Helianthus annuus* L.) leaves. *Acta Agr. Acad. Sci. Hung.* **32:** 5–15.

Herdi, F. (1983*b*): Histological changes in the leaf of sunflower (*Helianthus annuus* L.) in response to 2,4-D treatments. *Acta Agr. Acad. Sci. Hung.* **32:** 288–297.

Herdi, F. (1983*c*): The effect of 2,4-D on the petiole tissues of sunflower (*Helianthus annuus* L.). *Acta Phytop. Acad. Sci. Hung.* **18:** 63–77.

Herdi, F. (1983*d*): The influence of MCPA on the vascular tissue in the leaf petioles of sunflower (*Helianthus annuus* L.). *Acta Phytop. Acad. Sci. Hung.* **18:** 313–330.

Kiermayer, O. (1964): Growth responses to herbicides. In: L. J. Audus: *The Physiology and Biochemistry of Herbicides.* Academic Press, London–New York, 207–230.

Linck, A. J. (1976): Effects on the cytology and fine structure of plant cells. In: L. J. Audus: *Herbicides, Physiology, Biochemistry, Ecology,* Vol. **1.** Academic Press, New York–London, 83–125.

Meyer, R. E. (1970): Picloram and 2,4,5-T influence on honey mesquite morphology. *Weed Sci.* **18:** 525–531.

Murray, M. A., Whiting, A. G. (1947): A comparison of the effectiveness of 2,4-dichlorophenoxyacetic acid and four of its salts inducting histological responses in bean plants. *Bot. Gaz.* **109:** 13–39.

Pate, D. A., Funderburk, H. H., Lawrence, J. M., Davis, D. E. (1965): The effect of dichlobenil and dicamba on nodal tissues of alligatorweed. *Weeds* **13:** 208–210.

Pizzolato, T. D., Regehr, D. L. (1981): Anatomical effects of 2,4-DB on tomato internodes. *Can. J. Bot.* **59:** 1749–1760.

Sachs, T. (1975): Plant tumours resulting from unregulated hormone synthesis. *J. Theor. Biol.* **55:** 445–453.

Sorokin, H. P., Mathur, S. N., Thimann, K. V. (1962): The effects of auxins and kinetin on xylem differentiation in pea epicotyl. *Amer. J. Bot.* **49:** 444–454.

Tukey, H. B., Hamner, C. L., Imhofe, B. (1945): Histological changes in bindweed and sow thistle following application of 2,4-dichlorophenoxyacetic acid in herbicidal concentrations. *Bot. Gaz.* **107:** 62–73.

Watson, D. P. (1948): An anatomical study of the modification of bean leaves as a results of treatment with 2,4-D. *Amer. J. Bot.* **35:** 543–555.

Acta Botanica Hungarica 33 (1–2), pp. 139–150 (1987)

BOOK REVIEWS

Editor: G. FEKETE

EVENARI, M.–NOY-MEIR, I.–GOODALL, D. W. (eds): Hot Deserts and Arid Shrublands, Vol. 12. B. Elsevier Science Publishers, Amsterdam. 1986. VIII + p. 451.

This is the second part of a twin volume. Because of its length, the volume 12 of the series "Ecosystems of the World" edited by D. W. GOODALL, is published in two parts.

The first part (12A) has been published in 1985. It includes the general synthesis chapters, and regional descriptions of the hot deserts of America and Australia.

The volume 12B covers the hot deserts of Asia and Africa, and a concluding chapter.

As for geographical scope, this volume covers the hot deserts and arid shrublands of the Middle East, Arabian Peninsula, India, Africa and Madagascar. Interestingly enough, two regions (Iran and East-Africa) were left out. At the same time, the scopes of some chapters overlap each other in some degree. For example, the reader may get double presentation of the Sinai and Arabian desert. This gives a rare opportunity to see the same region and its biota from different aspects.

In a world, where the deserts are constantly extending their boundaries, consuming vast areas each year, it is extremely important to see and understand the original processes and strategies of the living organisms successfully established even in these types of hostile environment. This volume gives and abundant and overwhelming evidence that plant and animal life is really able to accommodate to these unbelievable extremities: excessive heat, over 50 °C; and cold, sometimes below 0 °C; extended dry periods, up to 10 months regularly or even years irregularly; short and intensive rainfall causing erosion; absence of pollinating animals, etc.

A desert organism has to invest more on maintenance, and the cost per unit of income is higher than in other areas, since the vital resources are spatially more scattered. The life in the desert is mainly controlled by a general scarcity of water and, frequently a scarcity of food as well. The concentration and availability of these resources vary greatly over time and in space, among years and within years. There are short periods of water and food abundance after rains; but timing, duration and level are variable and unpredictable.

At the same time, the deserts generally have every necessary conditions for a very high production, except water. Their ecological potential, providing the water supply, is often higher than that of the best agricultural regions of the world.

The descriptive chapters are the following. (1) The Deserts of the Middle East, by G. ORSHAN, covering: Sinai, Israel, Jordan, Syria, Iraq and N-Arabia with a complete water flow and standing biomass representation for the whole ecosystem. (2) The Deserts of the Arabian Peninsula, by A. A. ABD el RAHMAN. With some overall-landscape original photos and chart quadrat of 10×10 m showing the distribution of the vegetation of a wadi before and after rainfall. (3) The Thar Desert, by R. K. GUPTA, covering: the region between India and Pakistan. Including the connections of man and land use, ecological and economical relationships, changing land use due to new irrigation systems, introduced crops. (4) The Desert and Arid zones of Northern Africa, by H. N. LE HOUÉROU, covering: Marocco, Algeria, Tunisia, Libya, Egypt. Showing the vegetational changes of the last 80 years due to the climatic changes and overgrazing, the process of desertization. (5) Hot Deserts of Egypt and the Sudan, by M. A. AYYAD and S. I. GHABBOUR. With an Appendix of the Sinai. (6) The Sahel Zone North of the Equator, by TH. MONOD, covering: the famine-stricken southern belt of the Great Sahara from coast to coast. Including a provisional list of "Sahelian" plant and animal species. (7) The Namib desert, by H. WALTER. With good production data of different ecosystems. (8) The Karoo and Southern Kalahari, by M. J. A. WERGER. Adjoining

area to the previous one, with excellent illustrations. (9) The Arid Region of Madagascar, by W. RAUH. Richly illustrated with photos of one of the most curious vegetation of the world.

The last chapter (10) is "An Integrated View" of the hot desert ecosystems, by A. SHIMIDA, M. EVENARI and I. NOY-MEIR. It is really a conceptual summary of the twin volumes 12A and 12B. This is a bright presentation of the underlying ecological interconnections among the geographical and biological factors.

In each regional chapter, one can find mostly the same general outline: geographical, definition of the area, climate, geology, soil, soil-microorganisms, vegetation, phytogeography, animals, land use, man's impact, ecosystems.

The presentation is highly informative and attractive. Numerous black and white photos, drawings, maps and, tables make the text more alive. The references follow each chapter. At the very end there are four indices for the reader's convenience.

This volume is recommended highly to every theoretical and practical scientist and graduated students of ecology, especially to those who are concerned in the preservation, exploration and the possible future use of these immense "spare lands" of the Earth.

In the US/Canada the book is available from Elsevier Science Publishing Co. Inc., P. O. Box 1663, Grand Central Station, New York, N.Y. 10163.

Z. SZŐCS

C. NOZZOLILLO–P. J. LEA–F. A. LOEWUS (eds): Mobilization of Reserves in Germination. Recent Advances in Phytochemistry 17. Plenum Press, New York 1983, p. 312

Plants produce a wide variety of reproductive propagules designed to enable them to survive periodic harsh climatic conditions and to increase and multiply thereafter. The process of resurgence of growth of these small packages of genetic information is one of the wonders of life: the germination.

In this volume, germination of only one kind is considered: that of the seed of one-seed fruit of flowering plants. Seeds can contain large amounts of food reserves and for this reason are of fundamental importance to human society. Cultivation of seed-producing plants for purposes of human consumption or animal feeding are the basis of our agricultural activity, and the enduring interest shown by humans in the germination process. Germination of seeds is not a simple process and depends on many factors. Therefore a further delimitation of the topic to the interim period between the onset of germination, signaled by imbibition or uptake of water by the seed, and development of the independent plantlet, has been made.

Although many books and articles about germination have been published, our understanding of the process is far from being complete. This interdisciplinary volume presents some of the reactions involved in the transformation and translocation of reserve compounds and their final fate in the growing tissues.

The first step a reviving seed has to take is to hydrate its tissues and transform its membranes from their dormant resting state to an active state. The mechanism by which this is brought about is not fully understood and two major theses have been proposed. Both views are presented in this book. In Chapter 2, "Imbibition, Leakage and Membranes", E. W. SIMON and L. K. MILLS propose an interim "leaky" state as a result of rearrangement of phospholipids into a hexagonal phase. B. D. MCKERSIE and T. SERANATA in Chapter 3, "Membrane Structure in Germinating Seeds" uphold on the other side an opposite view that no fundamental change in membrane arrangement occurs and that "leakiness" can be explained sufficiently by physical chemistry alone.

The next phase is known as mobilization, including breakdown of reserves and their translocation to the growing parts of the young plant. The reserves are of three major types: carbohydrates, proteins and lipids.

Chapter 4, "Regulation of Nitrogen Metabolism during Early Seedling Growth" by A. OAKS, gives a detailed account on the processes of N-transport from the endosperm to the young seedling. Proteins constitute 10–16% of the dry weight of the cereal endosperm. They have two major fractions: prolamine and glutelin. They are the substrates for the peptide hydrolases which produce amino acids and peptides. These latter ones are the endogenous N-sources of the young plantlet during the first phase of development. On the other hand, the amino acids and peptides suppress the biosynthesis of amino acids in the embryo.

P. J. LEA deals with the other side of the same coin in the Chapter 5, "Amino Acid Interconversion in Germinating Seeds". He stresses the growing embryo may not have an absolute dependence on stored organic nitrogen, and small seed species may have an extremely limited supply of stored nitrogen. The developing seedling is approaching autonomy and

shows processes characteristic of the mature plant. This process of gradually becoming "independent" from the stored materials and energy is characterized in biochemical terms in details.

It is surprising, the agriculturally important species constitute less than 0.01% of the total number of known plant species, and even this small portion belongs to mainly two families only. This division represents, at the same time, the two major taxonomical divisions of the flowering plants: *Fabaceae* (*Leguminosae*) from among the dicotyledonous plants, and *Poaceae* (*Gramineae*) from the monocotyledonous ones. These families represent also two types of seeds in terms of stored materials. While the *Fabaceae* contain generally more protein than the others, the *Poaceae* can be characterized by a relative high carbohydrate content. The Chapters 4 and 5 deals with the protein of the seeds, while Chapters 6–8 are concentrated around the problems and processes of the carbohydrate content of the germinating seedlings.

In Chapter 6, "Starch-Lipid Complexes and Other non-Starch Components of Starch Granules in Cereal Grains", T. Gaillard reviews the different forms and compositions of the starch grains (amyloplastid), and the minor constituents of them, in particular the starch-bound monoacyl lipids.

In Chapters 7 and 8 the authors present several new findings about the fate and role of translocated sucrose in the developing pea seedling, and about the mobilization of endospermic mannan reserves of lettuce seeds, including an examination of the specific enzyme activities called into play.

F. A. Loewus stresses another aspect of germination, the energy-side of it. This is in connection with the phosphate-containing components of the seeds: phytin, myo-inositol, phytase and others. These questions are discussed in Chapter 9.

The complicated internal control mechanism of germination process is dealt in Chapters 11 and 10 by M. Black, R. S. Bandurski and others. They discuss the interactions among plant hormones, nucleic acids and membranes, the role of gibberellin activity, membrane permeability, auxin-transport, etc.

In the last Chapter, "Effect of Germination on Cereal and Legume Nutrient Changes and Food or Feed Value: a Review", P. L. Finney gives a detailed and overall picture on nutritive value of germinating seeds for human and animal consumption. It can be stated, it is the most prominent and promising aspect of germination. This excellent review of 70 pages can convince the reader of the great importance of the topic. The use of germinated seeds as an additional or preservative material to our food may reduce significantly our day's most serious problem: the malnutrition of millions caused by inadequate food of improperly balanced diets. Based on nearly 100 years of chemical studies, on about 70 years of animal feeding studies, on a few but well-documented human feeding studies, and on hundreds and in some cases thousands of years of experience by millions of people who have been living on it, it can be stated that carefully controlled germination of edible cereals and legumes is able of greatly alleviating today's food problems and avoiding tomorrow's food needs. The germinated seeds of our common agricultural plants are extremely rich in vitamins, proteins, fats, lipids, carbohydrates, minerals and many other components, moreover, many times all these constituents are nearly in optimal composition and ratios; one may say, they are especially designed for human consumption in a "home made" manner, with minimum cost and effort.

This volume can be valued highly as an up-to-date basis all those are interested in the plant physiological, biochemical, biophysical of nutritional aspects of germination.

Z. Szőcs

W. A. Côté (ed.): Biomass Utilization. Plenum Press, New York. 1983, p. 730

There is no doubt, the various ways of biomass utilization has became a certain focus of interest in our days. The shortage of food, feed, fiber and fuel in many areas of the world, the ever-increasing energy prices and the urgent need of environmentally safe technologies are the main driving forces behind this increasing attention.

On the other side, there are vast amounts of agricultural, industrial, municipal and other wastes and byproducts containing important organic matters without proper utilization. These wastes can be turned into valuable sources of energy, important chemicals, feed or even food. Many times these transformations may solve at the same time serious environmental problems, too.

This thick volume contains the proceedings of the Conference on Biomass Utilization, held in Alcabideche, Portugal from September 26 to October 9, 1982. The program was

organised as a comprehensive course on biomass utilization. We may say, it is really a comprehensive one. The 40 proceedings give an overall picture and in some field even a detailed review-type account of the state of the art and many future possibilities.

The material is arranged into six sections.

I. Biomass utilization — the concept

First D. O. Hall gives an overall picture of biomass sources and production, the energy use, the major biomass projects of the world, focusing the recent use and near future possibilities of converting biomass into fuels.

R. F. Ward discusses the problems of using biomass as food versus chemical feedstock or energy. He concludes biomass will have its greatest value when used as food for human consumption, less valuable for feeding animals or as chemical feedstocks and least for direct energy-conversion.

H. Sobel suggests that maximizing the use of biomass sources should be made with the population limits and keeping an eye on the "quality of life" (termed here by the daily industrial energy expenditure and daily individual biochemical calorie consumption). He urges to set limits to natural growth of human population especially in the Third World. His arguments are somewhat Malthusian and deterministic.

II. The raw material and its preparation
(The second section deals with biomass as a raw material)

T. Cunia emphasizes the necessity of a world-wide monitoring system based upon unified concepts and methods to keep watch over the present state and fate of biomass accumulated in the forests. This future forest inventory system would be of a great value because the overall biomass of the Earth is concentrated mainly in forests and in the tropical regions this biomass-pool is rapidly diminishing.

J. Kasile presents a practical example of using aerial photographic methods for estimating forest standing biomass from Ohio, USA.

G. Tsoumis gives a review of the different utilization pathways of forest biomass in Greece.

The present and future availability of different kinds of biomass such as grain crops, oilseed crops, latex-bearing crops, mill residues, molasses, manures etc. are discussed including a cost-benefit analysis of collection and transportation of them by W. J. Sheppard and B. Young for US and Canada.

The marine phytoplankton provide as much organic matter as all terrestrial vegetation, in the order of 10^{10} tons carbon per year. Their photosynthesizing capacity and efficiency ranks among the foremost in the plant world. They are rich sources for protein and many valuable chemicals of industrial and pharmaceutical importance. These aspects are reviewed by M. Indergaard.

A very promising new method of mass propagation of selected trees for biomass is presented by S. Venketeswaran and al. It is now possible through tissue culture techniques to produce "test tube trees", i.e. plants obtained from only a few cells of a treee by manipulations under laboratory conditions. Thus several thousand young plantlets can be produced from a single tree and these can be transferred to the field and grown as seedlings within a short time. In Texas, USA, there are experimental plantations of *Sapium sebiferum* Roxb., *Leucaena leucocephala* (Lam.) de Wit. and *Copaifera multijuga* Hayne. made by this technique.

Another promising future perspective of using microalgae as a source of biomass or H_2 for solar energy conversion are discussed by B. Mahro, L. H. Grimme and E. W. Becker.

Several papers deal with the problems of utilization of aquatic biomass such as algae, emergent macrophytes, floating weeds, seaweeds etc. for wastewater treatment especially for recycling polluting metals.

III. The structure and chemical composition of biomass

This section contains three papers concerning the anatomy, ultrastructure and chemical composition of wood, some structural characteristics of acid hydrolysis lignins and cellulose by W. A. Coté, E. J. Soltes and J. Papadopulos.

IV. Biological conversion methods

The new and old biotechnological methods are reviewed, fermentation techniques, single cell protein production on waste materials, biogas, composting and biofilm reactors by B. Pekin, J. C. Royer, S. Kirimhan and others.

V. Thermochemical conversion methods

E. J. Soltes discusses the different routes to chemicals, fuels and energy from forestry and agricultural wastes through diverse thermochemical processes: direct combustion, gasification, pyrolysis, tarification, etc. These are even now valuable opportunities to gain not only usable heat, but a variety of useful energy-dense fuels and/or chemical feedstocks. In the future, moreover, these ways may provide an alternative source of energy and chemicals instead of the diminishing sources of fossile oil, gas and coal.

A. A. C. M. Beenackers and W. P. M. Swaaij gives a "state of art" review on different possibilities of gaining methanol from wood. They discuss the experiences of the several pilote plants working in this field.

VI. Engineering and Economics in Biomass Utilization

This section contains eight papers mostly written from economical point of view or stressing the energy-side of the utilization processes. It can be seen from these analyses that the presently available possibilities of biomass utilization are mostly economical and profitable ways, highly advantageous for the environment and the man. A smaller portion of these ways are at the threshold of being profitable, while some others are promising, but needing further development and research. There is no doubt, many of these utilization processes could be much more accepted and widespread. The main hindrances are our ignorance, the rigidity of our industrial structure, the dependence on fossile fuels, and above all our narrow-minded industrially trained, money-centered thinking of way.

This valuable volums may help to broaden our vision about the possible healthy alternatives of development in utilizing the vast resources of the renewable sources of biomass in every form. There is a great need to change our value-system, our perspectives and expectations: to adapt our society to the limits and opportunities of the Earth, to value the renewable sources, to become more and more independent from the non-renewable ones, to find a healthy and balanced environmentally safe compromise between filling our needs and preserve the living system of the biologica sources: the soil, plants, animals and even our own health. It is very encouraging, to see in this excellent book, there are even now many well-functioning, living examples of these alternative, new ways of using the gift of Sun, the biomass.

We can highly recommend this book to everyone who is interested in the use of biomass, in the future ways of it or even in the present state of this art, both experts and students or interested readers of any kind.

Z. Szőcs

J. P. Gustafson (ed.): Gene manipulation in plant improvement — 16th Stadler Genetics Symposium. Plenum Press, New York and London, 1984. p. 668

The volume containing 24 lectures by excellent representatives of each scientific field provides a wide and thorough overview on the methods and prospects of plant breeding, including basic results of related plant sciences. It can be recommended not only for experts, but for any biologist interested in the topic.

The importance of plant breeding can hardly be overemphasized. As the first lecturer (G. W. Burton) fairly acknowledges, the main achievement was done by the primitive breeders who converted some weedy species into crops that efficiently feed the mankind.

Nevertheless as calculated by D. N. Duvick, during the last 60 years the contribution of modern plant breeding to the yield increase has been more than 50% for each crop, and it is still increasing in a linear fashion. One should be really impressed by this achievement.

S. Rajaram and G. S. Khush convince us about the importance of the international cooperation in plant improvement. They show how the two worldfamous breeding center, the CIMMYT in Mexico and the IRRI in the Philippines govern the breeding efforts for the tropical wheat and rice respectively.

These institutes collected thousands of varieties from the whole world, and apply all of the known modern breeding methods including multilocal testing, shuttle breeding, recurrent

selection, etc., producing widely adapted germplasm with high yielding stability, multiple resistance to diseases and tolerance to different environmental stresses. They deliver their varieties to developing countries, where local breeders can improve them further. The impact of IRRI on rice production is particularly outstanding, their varieties yield two or three times more than the traditional forms, often with shorter growth duration. Keeping in mind that rice is the most important food crop in the tropical countries, we have to akcnowledge that breeders have done their best, indeed for feeding the Third World.

In the subsequent studies, the authors mainly deal with the results of related fields somehow involved in the future of plant breeding.

D. C. RASMUSSON raises the question of ideotype research. Although it seems to be rather theoretical, he proves that this type of approach can be rewarding inspite of the ever present negative correlation.

L. T. EWANS, in his piece, emphasizes the difficulties of the physiological interpretation of those plant characteristics, which have major impact on yieldpotential, due to their complex and multigenic nature.

R. J. BAKER attempted to show that the study of quantitative genetics is closely allied with the practice of plant improvement, and could help the fine tuning of the selection strategies.

In A. L. HOOKER's taxonomic discussion on genomic (cytogenetic) classification of perennial *Triticeae* is particularly informative for wheat breeders, being this plant an interspecific allopolyploid hybrid. G. KIMBER's work on evolutionary relationships, measured by the level of chromosome pairing is closely connected to DEWEY's topic, as well as the next chapter by E. R. SEARS on mutation in wheat that raise the level of meiotic chromosome pairing. R. RILEY and C. N. LAW elegantly demonstrate the possibilies of chromosome manipulation (aneuploids, polyploids, substitutions) in plant breeding. M. D. BENETT in his excellent lecture on the nuclear architecture presents very exciting and up-to-date informations on the correlation between the location and expression of different genomes in the same nucleus.

Several authors deal with the different in vitro experimental technics applied in plant sciences, such as, embryo culture, in vitro pollination (G. B. COLLINS et al.) doubled haploids (P. S. BAENZINGER), protoplast fusion (E. C. COCKING), somaclonal variation (T. J. ORTON), selection from cell culture (C. P. MEREDITH). Inspite of the fact, that until now no cultivated variant has bred with the application of the above methods, these procedures are potentially very promising, enabling the breeders to overcome the sexual barriers, and to shorten the time to develop new variants.

The last five lectures including the molecular analysis of alien chromatin (R. APPELS and L. B. MORAN), genetic aspects of symbiotic nitrogen fixation (S. R. LONG), chloroplast gene manipulation (J. D. ROCHAIX et al.), gene expression in plants (R. N. BEACHY), plant transformation (J. R. BEDBROOK), summarize the recent results in plant molecular genetics. It is perhaps the most controversial part of the book. Genetic engineering raises overly high expectations, on one hand, and has to face vast scepticism on the other, mainly from the side of plant breeders. The reality certainly lies somewhere between these extremities. The genetic engineer is obviously able to isolate a single gene, transfer it, and make it express in an alien genome. However, the economically desirable traits are more complex (see EVANS), including genes of unknown number, which cannot be engineered at this stage. Nonetheless, single gene manipulation can be very useful, such as, transfering herbicide resistance (see ROCHAIX), or the ability to synthetise a particular compound.

In the last chapter N. W. SIMMONDS provides a comprehensive overview on the nature of plant breeding and its interactions with the underlying sciences.

I. TAKÁCS

J. BÁNHEGYI – S. TÓTH – G. UBRIZSY – J. VÖRÖS: Magyarország mikroszkopikus gombáinak határozókönyve 1–2 (Identification book for microscopic fungi in Hungary 1–2). Akadémiai Kiadó, Budapest, 1985

The authors of the work are leading personalities of the Hungarian mycology. Two of them, Dr. Gábor UBRIZSY, academician and Prof. Dr. József BÁNHEGYI — who initiated, prepared and in most part compiled the identification book — do not unfortunately live to see the appearance of this great work. It is also highly regrettable that while its manuscript had been completed more than ten years ago, this long-needed scientific work only appeared in 1985.

The identification book marks an important stage of the Hungarian mycology. As is read in the Preface "in the four-century history of the Hungarian mycology this is the first

attempt to process data of *Mycomycetes* for the whole territory of the country (and partly for adjacent areas within the Carpathian basin) with an almost monographic dullness, and publish them in the form of an identification book based on the most recent investigations and publications". It is also in the Preface that the authors of the book express appreciation of Gusztáv MOESZ, the Hungarian mycologist of name, without the important collecting, systematizing and critical activity of whom this work could not have been completed.

The system of fungi followed in the identification book is based on UBRIZSY–VÖRÖS' taxonomic conception. This system of fungi took the investigations of GÄUMANN, BESSEY, MARTIN, ALEXOPOULOS, GREIS, SPARROW, CHADEFAUD and AINSWORTH for basis, utilizing and contributing recent research results by SAVILE, KREISEL, von ARX, LODDER and others.

The identification book is divided in three volumes. The first volume discusses the phylum of *Myxomycotina*, and of the phylum *Eumycotina* the class of *Phycomycetes* and a part of the *Ascomycetes* (up to the *Discomycetes*). The *Ascomycetes* are continued in the second volume which then deals with the classes of *Basidiomycetes* and *Deuteromycetes*. The third — unpublished — volume of the identification book contains the indices.

The first volume begins with a chapter on Generals. In its first part fundamental conceptions of taxonomy and nomenclature are discussed at length, followed by the Phylogeny and system of fungi, in which the fungi are shown as an independent reign according to the modern view of systemization. The detailed treatment is introduced by the taxonomic key of families.

Beside the description of the species or group in question a good representation is invaluable in identifying microscopic fungi; moreover, a good drawing or photo may sometimes offer better orientation than even the most exact description. In the case of some groups of fungi (e.g. *Mycomycetes*, *Chytridiomycetidae*, *Pyrenomycetes*, *Discomycetes*, *Ustilaginales*) the material of figures backing the text of the key is particularly rich. Unfortunately, the same cannot be said for the order of *Moniliales*, although orientation in this system based on the way of conidium formation is almost hopeless without the aid of illustrations.

The bibliography lists numerous works of basic importance or comprehensive character. At the same time, works exposing the fungal flora of many areas in Hungary, or dealing with groups of fungi earlier unknown in Hungary are highly regrettably left out from the list.

In the end of the identification book a rich terminology for the microscopic fungi is found.

This identification book is indispensable in all special fields where microscopic fungi are either theoretically of practically dealt with.

J. GÖNCZÖL

T. MROZIŃSKA: Chlorophyta VI. Oedogonophyceae: Oedogoniales, in ETTL, H., GERLOFF, J., HEYNIG, H., MOLLENHAUER, D. (red.): Süßwasserflora von Mitteleuropa. Band 14. G. Fischer Verlag. Jena, 1985. p. 624

The monograph written by the well-known Polish algologist is the new volume of the series "Süßwasserflora von Mitteleuropa", a work planned to run to 24 volumes. The Polish algologist colleagues deserved the wide acknowledgement with the Flora Słodkowodna series compiled and edited by Professor STARMACH in which MROZIŃSKA's volume on *Oedogoniales* appeared in two editions (1969, 1984).

The structure of the monograph is the same as in the previous volumes. After the editors' preface a taxonomic key for the 20 classes of algae follows, which in accordance with the new conception published in 1984 enables the separation of the family *Oedogonophyceae*. In the first part of the book, following the author's preface, a concise characterization of the order *Oedogoniales* is given. The reader acquires knowledge of the shape of the cell, the structure of the cell-wall, the process of cell division. the growth of the thallus, the structure of the chloroplast and of the electron microscopic structure of the nucleus and pyrenoid. The ways of reproduction in the species of the order *Oedogoniales*, the vegetative reproduction and the sexual reproduction are described in detail, since without a knowledge of the different ways of reproduction, the phases of sexual reproduction, the formation and structure of antheridia, oogonia, oospores no accurate identification of the species would be possible. Some electron micrographs help in getting acquainted with them. The general part of the book is closed with short chapters on the phenology of the generative phase in the species *Oedogonium* and *Bulbochaete*, the distribution and collection of these species, and on the methods of examination of fresh and preserved samples.

The detailed treatment begins with a taxonomic key for the three genera of the single family in the order of *Oedogoniales*, and a brief characterization of the genus *Oedogonium*.

It is followed by a taxonomic key on 21 pages by means of which the 448 species of the genus can be identified. On the basis of the description and characterization of the species, using the drawings given for each species the reader can be convinced of the accuracy of identification. The separation of varieties and forms is made possible again by taxonomic keys. In this way exact knowledge can be acquired of actually much more than thousand taxa. Furthermore the author gives the habitats known so far for each taxon. Although according to its title the book gives account of freshwater *Oedogoniaceae* species only for Central Europe, the data of occurrence cover the whole world. In addition, data are found on the periods of sexual reproduction for almost every taxon, which is also very important for the accuracy of identification and for choosing the time of collecting. The description of the species of the genus is closed with a list of nearly 70 uncertain taxa.

Then the reader is made acquainted with 15 species of the genus *Oedocladium*, 113 species of the genus *Bulbochaete*, and with the subgeneric taxa in the above described manner.

The book is completed with a bibliography (427 works), a name index, and 1000 figures. Drawings are found for all species and for most varieties and forms. A figure often consists of 4–5 drawings.

It is regretted — though it does not detract from the author's merit — that the figures, and particularly the few electron micrographs, are typographically inferior to those found in the previous volumes.

The clear, logical structure, the precise description of the species, the rich material of illustration, the exact morphological treatment make MROZIŃSKA's book extremely useful for all specialists. Besides the algologists this excellent work is warmly recommended to systematists, and to biologists engaged in water management practice. Moreover, MROZIŃSKA's book cannot be dispensed within the university education either.

K. T. KISS

R. M. T. DAHLGREN, H. T. CLIFFORD, P. F. YEO: The Families of the Monocotyledons. Structure, Evolution and Taxonomy. Springer-Verlag, Heidelberg, 1985. p. 501

The result of a two-decade joint work of an international trio of authors is summed up in the book. It gives answer to long since existing doubts and problems concerning the evolution and systematization of monocotyledons with a many-sided approach based on the results of the most up-to-date investigations, whereby the monocotyledons are grouped in more definite and more homogeneous units. That these problems are not new in the history of botany is indicated by the dates of years in which the new taxa came into being. It is easy to see that most of them were described already in the last century; moreover, JUSSIEU placed the Asparaguses and Asphodeluses — among others — in a separate family as early as in 1789. With their latest results the authors mostly confirmed the observations made by their predecessors with a botanist's eye and heart. Some genera of the *Liliaceae*, the most heterogeneous family of all, have been raised to family level and included in a different order. At the same time, evolution genetic studies suggest, among others, that placing the *Orchideaceae* in a separate order is not justified. The taxonomic revision referred to has put an end to the intolerable situation that while the Asphodeluses, Trilliums and Tecophillas are discussed within the family *Liliaceae*, the phylogenetically much closer relatives of Orchideas, Alstroemerias and Irises were completely separated. The authors are the first to lay proper emphasis to the examination and exact determination of the character state, the known evolution genetic feature, which as a fundamental determinant of the evolutionary stage is decisive in constructing the phylogenetic model. That is why special importance is attached to a distinction between character state (with a common ancestor) and character condition (with independent line of evolution). Thus, the book contains the revision of the system of monocotyledons with the aid of evolution models based on the most up-to-date determination of the character state. The work is aimed, in essentials, at determining or estimating the origin of the characteristics, their native or acquired nature, with the view of producing more homogeneous taxa better reflecting their evolution. The authors' unconcealed intention is to break down the barriers of conventions and make an open-minded approach.

The authors first make the readers acquainted with the currently used system of morphological concepts, and with the possible evolution of the now visible forms. A special chapter based on the latest research results of JENSEN and NIELSEN deals with the chemical and biochemical characteristics of monocotyledons. It is followed by a detailed analysis of the possibilities of divergent and convergent evolution, and the likeliness of parallel evolution and reduction, then the recently accepted criteria of monocotyledons are listed. The conception and taxonomic importance of the character state is made easier to understand by the

representation of the rich diversity of plant organs. After an analysis of the character levels by organs and major taxa the first part of the book is closed with the demonstration of the assumed evolution of orders.

In the next part the latest evolution models of monocotyledons are seen. According to the course of evolution the currently existing representatives are grouped in 4 Complexes:

1. *Liliiflorae*,
2. *Ariflorae — Triuridiflorae — Alismatiflorae*,
3. *Bromeliiflorae — Zingiberiflorae — Comeliniflorae*,
4. *Areciflorae — Cyclanthiflorae — Pandaniflorae*.

In the third part, on nearly 400 pages, detailed description of the individual taxa is found in a taxonomic arrangement corresponding to the new viewpoints, a modification of of the authors' earlier system (DAHLGREN et CLIFFORD 1982) completed with recent results. The groups that form the above Complexes are placed by the authors in the Superorder, the highest unit below the class. Within the Superorders 23 orders were established according to the evolution models; in this work the international expert of the group (e.g. JAKOBSEN) also took part, if it was possible. On discussing the 10 superorders and the orders cytological, phytochemical, geo- and paleobotanical aspects are in each case touched upon. Most of the family names cover earlier described taxa re-established in compliance with priority, but in the case of 2 genera with differing courses of evolution reasons were found for promoting them to be families (*Blandfordiaceae, Doryanthaceae*). Several genera of the classical family of *Liliaceae* are raised to family level and placed in the *Asparagales* order, with their divergence from the order of *Liliales* underlined in a well arranged comparative table. For the families within the orders quite new keys are given in which a highly important role is played by the karyotype (p. 133). Seeing these excellent keys one inevitably feels a need of similar keys for higher and lower taxa. Since the primary aim of the book is to show the evolution and system of suprageneric taxa, lower level keys are by no means found wanted, but higher level ones are righteously called for, the more so because it is here in the first place that the new points of view would be seen to prevail. For taxa lower than the family names are no longer given; with the sub-families and tribes the author's names and years are regrettably omitted. The evolutionary processes and morphological details are made easy to understand by a multitude of precise drawings, figures and diagrams. The rich bibliography and name index would have been usefully completed by a subject index which would help in using the work as a text-book.

The excellent comprehensive work that contains the latest research results and theories concerning the systematization of monocotyledons is indispensable for botanists and botanical institutions, but those engaged in secondary and higher education as well as leaders of biological study circles may also profit by using it. This work so new in content and importance, quite unparalleled in the history of plant taxonomy, would by all means be worthy to be translated into Hungarian.

Z. KERESZTY

K. A. KERSHAW: Physiological ecology of lichens. Cambridge University Press, Cambridge, 1985, p. 293

The book is a new member of the series "Cambridge studies in ecology". As lichen symbionts combine advantageous features of two different organisms, physiological ecology joints two fields of biological sciences. Recently both physiology and ecology achieved considerable development also in the investigation of lichens. In the second half of this century significance of lichen communities in natural ecosystems became better recognized and studied, but our knowledge on this field has a lot of problems to solve, yet. These are ecological questions. Physiological ecology uses physiological methods, measures physiological parameters to answer these ecological questions. Recent results of lichen physiology make it possible to apply them in lichen ecology. This book provides an up-to-date critical and selective review of lichen physiological ecology. All the major factors in environment of lichens (gases of the air, minerals, water, light, temperature, etc.) is considered in connection with such important physiological processes like nitrogen fixation, photosynthesis or respiration. Physiological ecology can help us understanding why lichens are good indicators of air pollution, how they can exist in extreme dry, hot deserts or in extreme wet tropical rain forests, on rocks, stones containing high amount of heavy metals, how the symbiont partners help the lichens to live in different environmental circumstances. This book collects recent results of this field supplying a general basis for the researches of the following years. The author worked much in low

arctic conditions studying the vegetation of northern Canada where lichens are dominant components in the ecosystems. Many of the samples originate from his own work since data from other areas are very scattered. However these result can stimulate ecophysiological examinations of lichens living on other important parts of the world, e.g., in the tropical rain forests, in fog-induced communities, in "mossy" forests, etc. The author attempting a provisional speculative summary of the range of strategies which appear to be available to lichens intended to stimulate further work and discussion. This book serving well this aim is relevant to students and research workers in plant ecology, plant physiology and lichenology.

Edit Farkas

K. A. Kershaw and J. H. H. Looney: Quantitative and Dynamic Plant Ecology. 3rd edition. Edward Arnold, London, 1985. Price: £16.00

Let us start the review with a note concerned with the bibliographic data of this book. In fact, it has to be considered a first edition, even thogh the title is unchanged, since J. H. H. Looney appears for the first time as the co-author.

Unfortunately, there is much more that remained unchanged in comparison with the previous editions. There are chapters and lots of subchapters that have almost the same wording as in the 1964 edition. It is apparently in sharp contrast with the statement of the back cover, which says: "It is to the development of plant ecology itself that this edition is aimed". I think, in a rapidly changing field such as plant ecology, this goal cannot really achieved by leaving a considerable part of the text in a form presented 21 years before.

The back cover also promises some additions to the previous edition: "several techniques of ordination and classification . . . . . . are discussed in two new chapters". However, the reader does not get a balanced treatment of the subject of multivariate analysis. As far as ordination is concerned, the discussion is relatively satisfactory, the advantages of detrended correspondence analysis over principal components analysis are discussed in the last chapter (although without giving technical details of the methods). In charp contrast, the presentation of classification techniques is restricted to the divisive methods, either "early" or more advanced. The topic of agglomerative methods, although just as important as the preceding one, is set aside by two or three sentences.

Nevertheless, my overall impressions on the book are not as bad as the above notes might suggest. This book contains much useful information for both the student and the practicing scientist. Many questions raised in the text convince the reader that there is still much to do in vegetation science. Despite some typographical errors, the printing is of better quality than the former versions and the numerous figures are also nicely reproduced. Thus, it seems worthwhile to summarize the contents briefly.

The book falls into 12 chapters, plus appendices, references and a subject index. The first chapter deals with basic terms associated with the description of vegetation (life forms, stratification, variables). Then, we have an introduction to the statistical methods and sampling. This is perhaps the most disappointing part, just as in many similar texts, since the importance of decisions made during sample collection seems not realized and, in any case, the relationships between sampling and study objectives deserve much more attention.

Chapter 3 discusses plant succession and includes two new subchapters on more recent ideas concerning vegetational change. The next chapter, on cyclic changes, is updated by some new examples taken from the literature. Interspecific association and their casual factors (e.g., allelopathy) are covered in Chapter 5, also by presenting new examples.

Chapter 6 is concerned with population dynamics (events in the soil, establishment, growth, survival, etc.). The next chapter turns to the study of vegetation structure. Possibilities for the analysis of plant pattern are discussed, although most methods mentioned are relatively old. Potential factors responsible for a given spatial pattern are summarized in Chapter 8. These include plant morphology, environmental heterogeneities and interaction between plants.

Classification of vegetation gets into the focus in Chapter 9. The Braun-Blanquet school of phytosociology receives the most attention by the authors who suggest "to follow the traditional Braun-Blanquet approach . . . or to ordinate the data set with the association boundaries subsequently overlayed". They apparently reject the sophisticated clustering methods on the ground that classification "will always be prone to the limitations of field taxonomy as well as sampling error". However, it remains unexplained why the favoured methods are unaffected by these limitations.

Plexus techniques, the BRAY and CURTIS method of ordination and PCA are introduced in Chapter 10. Then, the so-called "arch-effect", an unavoidable concomitant of PCA when the underlying trend in the data is not linear, is illustrated. Novel techniques, such as DECORANA and TWINSPAN, are presented in the last chapter.

The usefulness of the book is increased throughout the text by the discussion of ecological implications of results. It is perhaps obvious from the above comments that this book is recommended for everybody interested in the "meaningful" interpretation of results, rather than for those unfamiliar with the technical details of methods.

J. PODANI

G. COOPER-DRIVER, T. SWAIN and E. E. CONN (eds): Chemically mediated interactions between plants and other organisms. Recent Advances in Phytochemistry. Volume 19. Plenum Press, New York, 1985. p. 246

This volume of the series contains the material of the 1984. Symposium of the Phytochemical Society of North America held in Boston. The subject is biochemical ecology. The authors include representatives of the most diverse branches of science: zoologists, parasitologists, botanists present their special viewpoints. What made it possible or even necessary for these fields of science to meet was the common object of examination: the plant and its secondary metabolic products. Focussing attention on them means a promising view, considering both the possibility of thorougher studies on global relations between living organism and practically: the co-operation of experts in various special fields.

The structure of the book is in complicance with the above conception. The centre is — naturally — the plant, its interactions with different organisms: a) pathogenic fungi, b) soil-microorganisms, c) other plants, d) insects, e) phytophagous mammals, are discused in turn.

It is difficult to give a brief formulation for the subject of the book. One of the reasons is the diversity of the content. Further, the articles differ also in depth. Beside summarizing articles reciting the literature of a narrower special field descriptions of concrete experiments are found. The depth to which the biochemical processes are treated shows similar changes. In a considerable part of the articles the possibility of agricultural utilization is also shown.

The subjects (grouped as mentioned above):

(a) The two phases of the defence of plants against pathogenic fungi: recognition and response are discussed in two papers. The authors analyse the defensive response of the plant cell to substances produced by the pathogenic organisms. They studied the specific receptors of these biochemical "signals" using genetic and immunological methods. Successive steps of the series of defensive reactions — phytoalexin production, cell-wall modification — are also specified (A. R. AYERS–J. J. GOODELL–P. L. DEANGELIS–L. L. CREASY).

(b) The microbe communities of the rhizosphere act on the plant in two ways: by taking part in the biological control of pathogens, and promoting the growth of the plant. Morphological and chemical description is given of the mechanism of the mycoparasites' entering and consuming the host organism that damages the plant. Similarly important is the process when the microbes colonizing the root surfaces drive out the pathogens through antibiosis or chelator mediated competition. When drawing final conclusions the authors duly consider the characteristics of soil (Y. ELAD–I. J. MISHAGI).

(c) The chapter on allelopathy is of summarizing nature. It gives a survey of science history reciting numerous observations and evidences. Compounds pointed out so far and the metabolic pathways related with them are included in a table. The role of allelopathy in agriculture (relation between weeds and cultivated plants) and natural ecosystems is approached from a practical side. Allelopathy takes part in shaping the pattern of vegetation, as well as determining the rate of succession by influencing the nitrogen fixation of the soil (E. L. RICE).

(d) A study of the relation between plants and phytophagous organisms on three trophic levels reveals that the plants signal the presence of the insect feeding on them to its natural enemies (parasites, pathogens, predators). The toxins accumulated in the insect, on the other hand, cause well detectable damages to the predator. It must by all means be emphasized that these "multichemical responses" are linked with the joint action of a multitude of plant compounds rather than with a single compound. This is analysed also by the examples of three plant families (P. BARBOSA–J. A. SAUNDERS–M. BERENBAUM–I. KUBO–F. J. HANKE).

(e) A highly interesting paper uses the snowshoe hare as an example of how the animal minimizes the quantity of plant toxins getting into its organism by diversified nutrition. This and the resource availability have an evolutionary influence on the concentration of

secondary metabolites in plant parts of various position and age; in general: it influences the defence strategies (J. P. BRIANT–F. S. CHAPIN III.–P. REICHARDT–T. CLAUSEN).

(f) Another interesting theory is the one about the pheromonal communication between plants. Trees exposed to stresses, e.g. chewing by worms, with the help of volatile compounds give information to the other members of the population. As a response, measurable defensive mechanisms begin to work in the intact trees too (D. F. RHOADES).

It would have been desirable to give a summary or say a few words about the debates held during the symposium. Little is seen of the effect the researchers exercised on each other's opinion, while there is much repetition within the same scope of subjects.

Not only specialists of any of the subjects discussed, or those hunting after novelties will find important sections in the volume. It contains the rudiments of fundamental questions which should be judged first of all according to their future importance. The problems discussed here formulate at the same time what kind of help is expected from the botanists. The book can in any case be recommended to those engaged in agricultural activities, as it may be of use in the control of insect pests, parasites and weeds.

Beáta OBORNY

The papers generally have the following components, which should be presented in the order listed:

1. Title, name of the author(s), affiliation, dataline, abstract, keywords
2. Text, acknowledgements
3. References
4. Footnotes
5. Tables
6. Figure captions
7. Illustrations

1. The *affiliation* should be as concise as possible and should include the complete mailing address of the authors. The date of receipt of the manuscript will be supplied by the editors. The abstract should be in English and should not exceed 250 words. It should clearly and simply summarize the most important methods and results. 5–10 significant expressions describing the content are used as keywords. Authors may recommend these keywords.

2. The *text* of the papers should be of high stylistic standard, requiring minor corrections only. The section headings, names of authors cited, latin names and terms should *not* be underlined or in capitals. Quantities should be expressed in SI-units.

3. *References* are accepted only in the Harvard system. Citation in the text must be as:
... (Jakucs 1961) ... or Jakucs (1961) ...
... (Fekete and Précsényi 1981) ...
... (Borhidi et al. 1979*a*) ...

The list of references should contain the names and initials of all authors (the abbreviation et al. is not accepted here); for *journal articles* year of publication, the title of the paper, title of the journal abbreviated, volume number, first and last pages.

For *books* or *chapters in books*, the title is followed by the publisher and place of publication. Book title words should be written with majuscules. Titles of papers published only in Hungarian should be translated in parentheses. All items are recommended to be cited both in the text and references.

Examples:

Jakucs, P. 1961: Die Phytozönologischen Verhältnisse der Flaumeichen-Buschwälder Südostmitteleuropas. Akadémiai Kiadó, Budapest.

Fekete, G., Précsényi, I. 1981: Niche structure of a perennial sandy grassland. In: Stefanovits, P., Berczik, Á., Fekete, G., Seidl, M. (eds): Man and the Biosphere Programme. Survey of 10 Years Activity in Hungary. Budapest, 68–102.

Borhidi, A., Muñiz, O., Del Risco, E. 1979*a*: Clasificación fitocenologica de la vegetación de Cuba. Acta Bot. Hung. **25**: 263–301.

Jakucs, P. 1973: „Síkfőkút Projekt". Egy tölgyes ökoszisztéma környezetbiológiai kutatása a bioszféra program keretein belül. (Síkfőkút-Project. Environmental-biological research of an oakwood ecosystem within the framework of the Biosphere program). MTA Biol. Oszt. Közl. **16**: 11–25.

4. *Footnotes* should be typed on a separate sheet.

5. *Tables* should be typed on separate pages. They should be numbered serially with arabic numerals and have a concise heading each. Vertical lines are not used. Clear wording of column heads is advisable.

6. *Figure captions* should de provided on a separate sheet.

7. *Illustrations* must not be inserted in the text. Figures will be redrawn. Therefore the most important point is the clearness of the figures, even pencil drawings are accepted (with a duplicate). Photographs should be sharp and well contrasted. All the illustrations should bear the figure number and author's name in pencil on the reverse.

*

The editors will send information to the first author about the arrival and *acceptance* of the paper. Two *proofs* will be provided, which are requested to be returned within 48 hours of receipt to the editor. Alterations in the text and especially in the illustrations are expensive and should be avoided. Hundred *offprints* are supplied free of charge.

These instructions are valid as from 1983.

Periodicals of the Hungarian Academy of Sciences are obtainable at the following addresses:

AUSTRALIA
C.B.D. LIBRARY AND SUBSCRIPTION SERVICE
Box 4886, G.P.O., *Sydney N.S.W. 2001*
COSMOS BOOKSHOP, 145 Ackland Street
St. Kilda (Melbourne), Victoria 3182

AUSTRIA
GLOBUS, Höchstädtplatz 3, *1206 Wien XX*

BELGIUM
OFFICE INTERNATIONAL DES PERIODIQUES
Avenue Louise, 485, *1050 Bruxelles*
E. STORY-SCIENTIA P.V.B.A.
P. van Duyseplein 8, *9000 Gent*

BULGARIA
HEMUS, Bulvar Ruszki 6, *Sofia*

CANADA
PANNONIA BOOKS, P.O. Box 1017
Postal Station "B", *Toronto, Ont. M5T 2T8*

CHINA
CNPICOR, Periodical Department, P.O. Box 50
Peking

CZECHOSLOVAKIA
MAD'ARSKA KULTURA, Národni třida 22
115 66 Praha
PNS DOVOZ TISKU, Vinohradská 46, *Praha 2*
PNS DOVOZ TLAČE, *Bratislava 2*

DENMARK
EJNAR MUNKSGAARD, 35, Nørre Søgade
1370 Copenhagen K

FEDERAL REPUBLIC OF GERMANY
KUNST UND WISSEN ERICH BIEBER
Postfach 46, *7000 Stuttgart 1*

FINLAND
AKATEEMINEN KIRJAKAUPPA, P.O. Box 128
00101 Helsinki 10

FRANCE
DAWSON-FRANCE S.A., B.P. 40, *91121 Palaiseau*
OFFICE INTERNATIONAL DE DOCUMENTATION ET LIBRAIRIE, 48 rue Gay-Lussac
75240 Paris, Cedex 05

GERMAN DEMOCRATIC REPUBLIC
HAUS DER UNGARISCHEN KULTUR
Karl Liebknecht-Straße 9, *DDR-102 Berlin*

GREAT BRITAIN
BLACKWELL'S PERIODICALS DIVISION
Hythe Bridge Street, *Oxford OX1 2ET*
BUMPUS, HALDANE AND MAXWELL LTD.
Cowper Works, *Olney, Bucks MK46 4BN*
COLLET'S HOLDINGS LTD., Denington Estate,
Wellingborough, Northants NN8 2QT
WM DAWSON AND SONS LTD., Cannon House
Folkstone, Kent CT19 5EE
H. K. LEWIS AND CO., 136 Gower Street
London WC1E 6BS

GREECE
KOSTARAKIS BROTHERS INTERNATIONAL BOOKSELLERS, 2 Hippokratous Street, *Athens-143*

HOLLAND
FAXON EUROPE, P.O. Box 167
1000 AD Amsterdam
MARTINUS NIJHOFF B. V.
Lange Voorhout 9-11, *Den Haag*
SWETS SUBSCRIPTION SERVICE
P.O. Box 830, 2160 Sz Lisse

INDIA
ALLIED PUBLISHING PVT. LTD.
750 Mount Road, *Madras 600002*
CENTRAL NEWS AGENCY PVT. LTD.
Connaught Circus, *New Delhi 110001*
INTERNATIONAL BOOK HOUSE PVT. LTD.
Madame Cama Road, *Bombay 400039*

ITALY
D. E. A., Via Lima 28, *00198 Roma*
INTERSCIENTIA, Via Mazzé 28, *10149 Torino*
LIBRERIA COMMISSIONARIA SANSONI
Via Lamarmora 45, *50121 Firenze*
SANTO VANASIA, Via M. Macchi 58
20124 Milano

JAPAN
KINOKUNIYA COMPANY LTD.
Journal Department, P.O. Box 55
Chitose, *Tokyo 156*
MARUZEN COMPANY LTD., Book Department
P.O. Box 5050 Tokyo International, *Tokyo 100-31*
NAUKA LTD., Import Department
2-30-19 Minami Ikebukuro, Toshima-ku, *Tokyo 171*

KOREA
CHULPANMUL, *Phenjan*

NORWAY
TANUM-TIDSKRIFT-SENTRALEN A.S.
Karl Johansgata 43, *1000 Oslo*

POLAND
WĘGIERSKI INSTYTUT KULTURY
Marszalkowska 80, *00-517 Warszawa*
CKP I W, ul. Towarowa 28, *00-958 Warszawa*

ROUMANIA
D. E. P., *Bucuresti*
ILEXIM, Calea Grivitei 64-66, *Bucuresti*

SOVIET UNION
SOYUZPECHAT — IMPORT, *Moscow*
and the post offices in each town
MEZHDUNARODNAYA KNIGA, *Moscow G-200*

SPAIN
DIAZ DE SANTOS Lagasca 95, *Madrid 6*

SWEDEN
ESSELTE TIDSKRIFTSCENTRALEN
Box 62, *101 20 Stockholm*

SWITZERLAND
KARGER LIBRI AG, Petersgraben 31, *4011 Basel*

USA
EBSCO SUBSCRIPTION SERVICES
P.O. Box 1943, *Birmingham, Alabama 35201*
F. W. FAXON COMPANY, INC.
15 Southwest Park, *Westwood Mass. 02090*
MAJOR SCIENTIFIC SUBSCRIPTIONS
1851 Diplomat, P.O. Box 819074,
Pallas, Tx. 75381-9074
READ-MORE PUBLICATIONS, INC.
140 Cedar Street, *New York, N. Y. 10006*

YUGOSLAVIA
JUGOSLOVENSKA KNJIGA, Terazije 27, *Beograd*
FORUM, Vojvode Mišića 1, *21000 Novi Sad*

Index: 26.006

ACTA BOTANICA

A QUARTERLY OF THE HUNGARIAN ACADEMY OF SCIENCES

Acta Botanica publishes original reports on botanical subjects in English, French, German, Spanish and Russian

Acta Botanica is published in yearly volumes of four issues by

AKADÉMIAI KIADÓ
Publishing House of the Hungarian Academy of Sciences
H-1054 Budapest, Alkotmány u. 21.

Manuscripts and editorial correspondence should be addressed to
Acta Botanica 1363 Budapest P.O. Box 24

Subscription information

Orders should be addressed to

KULTURA Foreign Trading Company
1389 Budapest P.O. Box 149

or to its representatives abroad

Acta Botanica Hungarica is abstracted/indexed in Biological Abstracts, Chemical Abstracts, Current Contents–Agriculture, Biology and Environmental Sciences, Excerpta Botanica, Excerpta Medica

© Akadémiai Kiadó, Budapest

INSTRUCTIONS TO AUTHORS

Papers will be considered for publication in *Acta Botanica Hungarica* only if they have not previously been published or submitted for publication elsewhere. They may be written in English, French, German, Russian or Spanish. From Hungarian authors papers are also accepted in Hungarian.

Manuscripts should be sent to

Prof. Pál Jakucs
editor-in-chief
Ecological Department,
Kossuth Lajos University,
H-4010 Debrecen

or to

Prof. Attila Borhidi
managing editor
Botanical Institute of the
Hungarian Academy of Sciences
H-2163 Vácrátót

Form of manuscript

Manuscripts should be typewritten in duplicate, double-spaced, 25 lines with 50 letters on each page. Articles should in general not exceed 25 typed pages tables and illustrations included. Acceptance depends on the opinion of one or more referees and the decision of the Editorial Board. Papers accepted for publication are subjected to editorial revision.

CONTENTS

PRINTED IN HUNGARY

Akadémiai Kiadó és Nyomda Vállalat, Budapest

Acta Botanica Hungarica 33 (3—4), pp. 151—185 (1987)

THE MAIN VEGETATION UNITS OF CUBA

A. Borhidi

INSTITUTE OF ECOLOGY AND BOTANY, HUNGARIAN ACADEMY OF SCIENCES, H-2163 VÁCRÁTÓT, HUNGARY

(Received: 10 October 1983)

The vegetation map of Cuba was prepared at a scale of 1 : 1 000 000 and published by A. Borhidi and O. Muñiz in 1980 (see: Acta Bot. Acad. Sci. Hung. 26: 25–53) in German language and later also in Spanish (1984), both with a short qualitative description of the vegetation units distinguished on the map. In this article the principal structural, floristic, ecological and chorological features of the most common units of the vegetation of Cuba are discussed. These are the following units: I. Rainforests: submontane, montane, sclerophyllous montane, elfin forests. II. Seasonal evergreen forests; lowland, submontane; III. Semi-deciduous forests: mesophytic, xerophytic; IV. Tropical karstic forests: Species rich western, species poor western, eastern, montane; V. Dry forests and shrubwoods: dry evergreen forests, dry thorny limestone shrubwoods, dry lowland serpentine shrubwoods, semidry lowland serpentine shrubwoods. VI. Humid montane shrubwoods: Sclerophyllous serpentine montane shrubwoods, elfin thickets; VII. Semi-desert vegetation: Cactus scrub; VIII. Coniferous forests and woodlands with several subtypes; IX. Savanna and grassland vegetation: with tall palms and grasses, with dwarf palms and short grasses; with deciduous trees, treeless savannas; X. Freshwater vegetation: Alluvial forests, riverain forests, swamp vegetation, freshwater weed vegetation; Coastal vegetation: mangroves, sandy beaches, rock pavement vegetation.

On the vegetation map of Cuba (Borhidi and Muñiz 1980, 1984) the following formations, vegetation units and subunits are mapped:

A) Rainforests or ombrophilous forests

a. submontane
b. wet montane
c. semi-dry or sclerophyllous montane on serpentine
d. elfin forests

B) Montane shrubwoods and thickets

a. semi-dry or sclerophyllous montane shrubwoods on serpentine
b. elfin thickets

C) Seasonal evergreen forests

a. lowland
b. submontane

D) Semi-deciduous forests

a. mesophytic
b. xerophytic

E) Tropical karstic forests

a. western, species rich
b. western, species poor
c. eastern
d. montane

F) Dry forests and shrubwoods

a. dry evergreen forests
b. dry thorny limestone shrubwoods
c. dry thorny serpentine shrubwoods
d. semi-dry serpentine shrubwoods

G) Semi-desert vegetation

a. Cactus scrub

H) Coniferous forests and woodlands

a. Pinus tropicalis woodland on sand
b. Pinus tropicalis-caribaea woodland on slate
c. Mixed oak-pine forest
d. Pinus caribaea forest on serpentine
e. Pinus cubensis forests on serpentine
  ea. xerothermic
  eb. mesophilous and montane
f. montane tree-fern–pine woods

I) Savannas

a. tall palm savannas
  aa. Roystonea-Ceiba agricultural
  ab. Roystonea agricultural
  ac. Copernicia agricultural
  ad. Sabal natural edaphic
  ae. Sabal secondary
b. dwarf palm savannas
  ba. Coccothrinax and Copernicia on serpentine
  bb. Acoelorrhaphe on sand
c. pine savannas
d. deciduous and treeless savannas

J) Freshwater vegetation

a. alluvial forests
b. riverain forests
c. swamp vegetation complex
d. fresh water weed vegetation

K) Coastal vegetation

a. mangroves
b. sandy beaches
c. littoral rock pavement

The short description of the structural, floristic, ecological and chorological features of these units is the following:

RAINFORESTS

Submontane rainforests (*Calophyllo–Carapetum guianensis*)

Forests with three canopy layers occurring on yellowish red mountain soils in the Moa Mts and in the Toa, Jaguani and Duaba basins where precipitation is more than 2500 mm and is evenly distributed over the year. The upper canopy layer is 30–35 m high, almost completely closed. As in the Mora forests of Trinidad (Beard 1946), this layer is composed of a single species, which in Cuba is *Carapa guianensis*. It is very rarely mingled with some exceptionally tall specimens of second level constituents. The plank buttresses of *Carapa guianensis* are frequently entwined by the aerial roots of the strangler *Clusia rosea*. The fully closed middle layer is 20–25 m high, and is composed of numerous tree species, whose leaves are mostly mesophylls. Permanent elements are *Calophyllum utile*, *Sloanea curatellifolia*, *Dipholis jubilla*, *Guarea guidonia*, *Cupania americana*, *Buchenavia capitata*, *Ficus wrightii*, and *Roystonea regia*. Of the montane elements *Ocotea leucoxylon* and *Phoebe montana* are mentioned. *Cecropia peltata*, *Didymopanax morototoni* and *Ochroma pyramidalis* occur in the cleared habitats. Palms are commonly found between the second and third layers along creekes, e.g. *Bactris cubensis*, *Prestoea montana* and *Calyptronoma clementis* ssp. *orientensis*. Such stands rich in palms are popularly referred to as "Manacales" (see León 1946: 61). The third canopy layer is 6–15 m high, and is only up to 50–60% closed. It is very rich in species, some characteristic elements being *Oxandra lanceolata*, *O. laurifolia*, and the big leaved *Cordia sulcata*, *Miconia elata*, *M. dodecandra*, and tree ferns, such as *Cyathea araneosa* and *Cnemidaria horrida*. The tree-sized herbaceous life form is also typical (*Heliconia caribaea*). In the sparser shrub layer *Cassipourea elliptica*, Myrtaceae and Melastomataceae species are abundant. The herb layer is dominated by ferns, *Ichnanthus pallens*, *Scleria pilosissima* and *S. secans* in the more moist places. Few macrophyllous lianes occur, e.g. *Omphalea diandra* and *Marcgravia evenia*. The double epiphyte layer is rich, the upper being dominated by flowering plants (*Columnea tincta*, *Psychotria nutans*, *Hillia tetrandra*, *Maxillaria* species, *Laelia lyonsii*, *Reichenbachianthus emarginatus*, *Aechmea nudicaulis*, *Hohenbergia penduliflora*, *Guzmania monostachya* and *G. lingulata*. The lower epiphyte layer is composed primarily of ferns, e.g. *Elaphoglossum crinitum*, *Rhipidopteris peltata*, *Polypodium*, *Asplenium* and *Trichomanes* species, and *Lycopodium funiculum*. Forest communities with similar structure are the *Sloanea berteriana–Ormosia krugii* association described by Ciferri (1936) from Hispaniola, the *Dacryodes–Sloanea* community in Dominica (Beard 1949), also reported from Puerto Rico (Dansereau 1966) and Guadeloupe (Stehlé 1945) and the *Psidium montanum* – *Calophyllum jacquinii* community described from Jamaica by Asprey and Robbins (1953).

Wet montane rainforests (*Ocoteo–Magnolietalia*)

This is the climax vegetation zone over 800 m altitude in Sierra Maestra, Escambray Mts and Sierra del Purial, and also in some mesoclimatic spots in Moa, Sierra de Cristal and Baracoa. Annual precipitation is 1700–3000 mm, distributed evenly over the year, the average temperature is 14–22 °C. Yellowish red latosolic soils and montane yellow soils predominate. Two canopy layers can be recognized. These rainforests correspond to the "fangales" (León 1946: 62), the "high open forests" (Seifriz 1943) and are called the "montane mist forests" in Jamaica (Asprey and Robins 1953). They are 20–25 m high and have a closed upper layer consisting of microphylls and notophylls, e.g. *Magnolia cubensis*, *Ocotea cuneata*, *O. leucoxylon*, *O. floribunda*, *Myrsine coriacea*, and *Cyrilla racemiflora*. Characteristic trees in the second layer are *Clusia tetrastigma*, *Gomidesia lindeniana*, *Alchornea latifolia*, *Garrya fadyenii*,

Fig. 1. Perfile of a montane rain forest stand in the Sierra Maestra, Alto de Cardero, 1300 m. (Made by A. BORHIDI, O. MUÑIZ and S. VAZQUEZ, 1969, original) Ca = *Cyathea arborea* and spp.; Cr = *Cyrilla racemiflora;* Ct = *Clusia tetrasperma;* Gf = *Garrya fadyenii;* Hh = *Hemitelia horrida;* La = *Laplacea angustifolia;* Lq = *Lophosoria quadriradiata;* Mc = *Magnolia cubensis;* Md = *Matayba domingensis;* Ml = *Meriania leucantha* ssp. *nana;* Mp = *Miconia punctata;* Oc = *Ocotea cuneata;* Ol = *Ocotea leucoxylon;* Ox = *Oxandra laurifolia;* Ps = *Persea similis;* Rf = *Rapanea ferruginea;* Tm = *Talauma minor;* To = *Tabebuia oligolepis;* Trm = *Ternstroemia monticola;* Vl = *Vaccinium leonis;* Wp = *Weinmannia pinnata*

Fig. 2. Montane rain forest on the Turquino Peak, at 1700 m. with tree ferns in the second canopy (Photo: A. BORHIDI)

Miconia punctata, and *Ossaea ottoschmidtii*, and tree ferns, such as *Cyathea arborea*, *C. balanocarpa* and *C. cubensis*. The two epiphyte layers are very rich, having orchids and bromelias (e.g. *Pleurothallis* species, *Guzmania lingulata*, *G. monostachya*, *G. erythrolepis*, *Tillandsia* species, *Vriesea* species, *Catopsis* species, and *Dilomilis montana*) in the upper, and in the lower epiphyte ferns (*Polypodium*, *Elaphoglossum*, *Hymenophyllum* and *Trichomanes* species), epiphyllous mosses and liverworts. Terrestrial orchids (*Prescottia*, *Ponthieva*, *Malaxis*, and *Phaius*) and shade-tolerant lianes (*Odontosoria*, *Gleichenia*, *Peperomia*, and *Schradera* species) are characteristic of the herb layer. The *Magnolio–Laplaceetum angustifoliae* community developed in Sierra Maestra between 800–1600 m represents a relatively rich rainforest type characterized by *Torralbasia cuneifolia*, *Solonia reflexa*, *Ditta maestrensis*, *Brunellia comocladifolia*, *Weinmannia pinnata*, *Lasianthus lanceolatus*, *Cleyera nimanimae*, *Graffenrieda rufescens*, and *Ilex macfadyenii;* it has very diverse epiphyte layers. Secondary communities with *Prestoea montana* and ferns dominating the herb layer, are typical following deforestation or wind damage between 800–1200 m (e.g. Grand Piedra). A poorer community with a less montane character is the *Magnolio–Cyrilletum racemiflorae* developed in the Escambray Mountains between 800 and 1100 m, it often occurs as extrazonal stands. Submontane elements and some endemics of the herb and shrub layers, such as *Pilea clarana*, *P. cellulosa*, *P. clementis*, and *Psychotria martii*, are typical.

Semi-arid or sclerophyllous montane serpentine rainforests (*Podocarpo–Sloanetalia*)

These forests represent the climax vegetation type in the Cristal and Moa mountains between 400 and 900 m elevation. Extrazonal stands are found in the valleys of Nipe Mts. Climatic requirements are: annual precipitation 1800–3200 mm, with rainfall all year round,

and a mean temperature of 18–24 °C. Two canopy layers are recognized, the constituents being sclerophyllous and lauraceous trees and shrubs. The open, 15–22 m high upper canopy layer is composed of *Calophyllum utile*, *Podocarpus ekmanii*, *Hyeromina nipensis*, *Dipholis jubilla*, *Cyrilla cubensis* ssp. *nipensis*, *Pera ekmanii*, *Ocotea leucoxylon*, *O. bucheri*, *Tabebuia dubia*, *Byrsonima coriacea* and *B. orientensis*, *Matayba domingensis*, *Bonnetia cubensis*, *Talauma minor* ssp. *oblongifolia*, and *Magnolia cubensis*, often mingled with *Pinus cubensis*. The lower stratum is 5–12 m high and more closed. Abundant species are *Linociera domingensis*, *Tetrazygia bicolor*, *Spathelia pinetorum*, *Tapura cubensis*, *Byrsonima biflora*, and *Ilex berteroi*. A constant element is *Bactris cubensis*, and the tree fern *Alsophila aquilina*. In the shrub layer *Psychotria moaensis*, *Myrcia gundlachii*, *Rauvolfia salicifolia*, *Moacroton ekmanii*, *Baccharis shaferi*, *Shafera platyphylla*, and *Eugenia*, *Lyonia*, *Ossaea*, *Calycogonium*, *Eupatorium*, and *Vernonia* species are typical. Due to the openness of the canopy layers the epiphyte levels are less clear-cut and poorer, with small orchids (*Dilomilis elata*, *D. oligophylla*, *Polystachya luteola*, *Dichaea hystricina*, *Dinema cubincola*, *Epidendrum globosum*, *Lanium hiorami*, *Comparettia falcata*, *Elleanthus linifolius*) predominating. The shade-tolerant epiphytes and epiphyllous bryophytes are absent, the number of ferns is much reduced. By contrast, many lianes grow in these forests, e.g , *Morinda moaensis*, *Vanilla wrightii*, *Gleichenia flexuosa*, *G. leonis*, *Chusquea abietifolia*, *Arthrostylidium* species, *Odontosoria* species, *Schradera cubensis*, *Marcgravia evenia*, *Rajania baracoensis*, *Eupatorium rhexioides*, *Lygodium volubile*, and *Platygyne obovata*, etc. The forests of this vegetation belt have been classified into two cenological noda. The broad-leaved climax forests belong to the *Podocarpo–Byrsonimion orientensis* nodum with several associations. The non-climax woodlands, in which pines are dominant, have been assigned to the *Cyrillo–Pinion cubensis* alliance. The latter one is a more humid community having luxuriant herb and moss strata and relatively rich epiphyte layer. Noted discriminating species are: *Senecio rivalis*, *S. polyphlebius*, *Hedyosmum crassifolium*, *Cladium restioides*, *Rhynchospora marisculus*, *Scleria secans*, *Calyptronoma clementis* ssp. *orientensis*, *Isachne leerzioides*, *Rondeletia pachyphylla*, *Gundlachia cubensis*, *Brya subinermis*, and *Pilea* species.

Elfin forests or mossy forests (*Weinmannio–Cyrilletalia*)

In Cuba this type is confined to the high altitude belts of Sierra Maestra, and to the high mountains of the Pico Turquino and Pico Bayamesa group between 1600–1900 m. In frost-free, evenly cool moist climate it is a climax type, but extrazonal stands on moist gravel slides may also occur. The annual mean temperature required is 10–14 °C, the total rainfall is 2800–3200 mm per year. This type is partly identical with the "monte fresco" described by León (1946: 63), but this statement does not hold for the stand shown in Fig. 33. The "alpine thicket" (Seifriz 1943), the "elfin woodland" (Beard 1944, 1955, Asprey and Robbins 1953), the "montane shrub zone" (Dansereau 1966) and, in part, the "foresta montana" (Ciferri 1936) appear to be synonymous. In the Antillean islands mossy forests are found at very different altitudes: in the Lesser Antilles as low as at 300 m (Beard 1949), in Puerto Rico between 1000 and 1200 m (Howard 1968, 1969), in Jamaica between 1600–2000 m, and in Hispaniola over 2000 m. The canopy layer is closed, very dense, 6–12 m high. The constituents include small-leaved sclerophyllous and leaf-succulent twisted trees and tree ferns reaching the canopy level. The shrub layer is also dense, an almost impenetrable bush tangled by pteridophytic lianes, such as the *Dennstaedtia*, *Odontosoria* and *Gleichenia* species. Species characteristic of the canopy layer are *Myrsine microphylla*, *Nectandra reticularis*, *Sapium maestrense*, *Persea anomala*, *Symplocos leonis*, *Eupatorium* (*Ageratina*) *paucibracteatum*, *Cyrilla racemiflora*, *Weinmannia pinnata*, *Torralbasia cuneifolia*, *Garrya fadyeni*, *Vaccinium leonis*, *Cyathea arborea*, *C. balanocarpa*, *C. minor*, *Alsophila aspera*, and *Lopho-*

Fig. 3. Elfin forest on the Turquino Peak (Sierra Maestra) at 1850 m (Photo: A. BORHIDI)

soria quadriradiata. Examples for the abundant shrub layer plants are *Lyonia calycosa, Ternstroemia monticola* and *T. leonis, Miconia turquinensis, M. nystroemii, Duranta fletcheriana, Cordia longipedunculata, Tabebuia turquinensis, Hedyosmum cubense, Henriettea ekmanii,* and *Scolosanthus maestrensis.* Ferns and lycopods, such as *Cheilanthes harrisii, Diplazium urbanii, Blechnum tuerckheimii, Danaea* species, *Lycopodium clavatum, L. serrulatum, L. taxifolium,* and *L. montanum,* are dominant in the herb layer. The simple epiphyte stratum is very rich in small endemic orchids (e.g. *Lepanthes ekmanii, L. ovata, L. fractiflexa, L. fulva, L. leonis, Stelis cubensis, Pleurothallis* spp.) in Hymenophyllaceae species (six *Trichomanes* and four *Hymenophyllum* species occur), *Polypodium* and *Elaphoglossum* species. The soil surface, the branches and the lower foliage of trees are covered by an unbroken stretch of bryophytes, including nearly 40 mosses, such as *Meteoriopsis patula, Mettenothamnium reptans, Macromitrium harrisii, M. jamaicense, M. schwaneckeanum, Hypnum polypterum, Phyllogonium fulgens, Pilotrichella flexilis, Prionodon densus, Rhizogonium spiniforme,* and *Fissidens weizii,* etc. Only one community type in Cuba may be assigned to this cenological category, namely the *Myrsino (microphyllae)–Nectandretum reticularis* association, which is extremely rich in endemics (they account for 41.15% of the non-zero scores in the data).

Semi-arid or sclerophyllous montane serpentine shrubwoods (*Clusio–Ilicetalia*)

Microphyllous evergreen montane shrubwoods have been reported to be present on young lava soils of Central American volcanoes (LÖTSCHERT 1959) and on the slopes of the Blue Mountains in Jamaica, in a mesoclimatically arid zone (ASPREY and ROBBINS 1953).

These two noda, under the respective names *Myrico–Baccharidetalia vaccinioides* and *Myrico–Lyonietalia jamaicensis*, have been amalgamated into the class *Myrico–Baccharidetea* (KNAPP 1965, see also KNAPP 1965: 297). However, the montane serpentine shrubwoods of Cuba, often called as "charrascals", are completely different from these in floristic composition and seral position. The Cuban shrubwoods are not pioneer communities, unlike those in Central America, and not subclimax types of arid regions, unlike the sclerophyllous montane shrubwoods of Jamaica. The montane shrubwoods in the Nipe, Cristal and Moa mountains are edaphic climax communities developed under a humid tropical rainforest climate. Their sclerophyllous character is a mere consequence of the ferritic soils derived from serpentine bedrocks. The overwhelming majority of species are endemic so that a separate class, *Clusio–Ilicetea*, was created to include these communities. It consists of a dense bush of microphyllous and nanophyllous sclerophyll shrubs and stunted trees up to 4–6 m height, with an open layer of emergent trees reaching 7–10 m height. In Moa this community has high species diversity between 600 and 1000 m in altitude. The more moist association group of Moa (*Ilici–Laplaceion*) is characterized by the following trees and shrubs: *Ilex berteroi, I. victorini, I. hypaneura, I. shaferi, Laplacea moaensis, L. benitoensis, Clusia moaensis, C. callosa, C. monocarpa, Acrosynanthus trachyphyllus, Rauvolfia salicifolia, Byrsonima biflora, Lyonia glandulosa, Cyrilla cubensis, Tapura cubensis, Myrica shaferi, Antirhea abbreviata, Alsophila aquilina, Jacaranda arborea, Illicium cubense*, and *Rheedia polyneura*, etc. Only a few epiphytes occur (*Dilomilis oligophylla, Polypodium duale, Hymenophyllum abruptum*). Conversely, the sclerophyllous lianes are numerous (e.g. *Arthrostylidium fimbriatum, A. pinifolium, Feddea cubensis, Rajania baracoensis, Symphysia alainii, Morinda moaensis*, etc.). *Ekmanochloa aristata, Paepalanthus pungens, P. riparius, Rhynchospora cernua, R. pruinosa*, and *R. shaferi* are characteristic of the herb layer in cleared areas. The contribution of endemic taxa to the total of all scores is 77%. In Nipe on Loma Mensura at 650–1000 m the *Myrcio–Bourrerietum* association is found, which is similar in appearance but more xeromorphic, having many spinose elements (here the contribution of endemics to the total is 70%, also very high!). Characteristic species are *Bourreria pauciflora, Myrcia retivenia, Coccoloba reflexa, Spathelia cubensis, Callicarpa lancifolia, Ariadne shaferi* ssp. *shaferi, Clusia nipensis, Annona sclerophylla, Calycogonium rosmarinifolium, Euphorbia podocarpifolia, Jacaranda arborea, Eugenia mensuraensis*, and *Baccharis shaferi*. There are few lianes, the endemic *Harnackia bisecta* is characteristic. In the herb layer some drought-resistant terrestrial orchids (*Bletia purpurea, B. florida, Encyclia atropurpurea*) and many cyperaceous species are found.

Elfin thickets (*Ilici–Myricion cacuminis*)

This vegetation type is represented by extrazonal stands on the southern and eastern bluffs between 1800 and 1970 m in Pico Turquino, the highest mountains of Sierra Maestra. It corresponds to the "alpine thicket" described by BEARD (1944, 1955), the "alpine woodland" of HOWARD (1969) and is on a par with the Central American alpine shrublands that are rich in Ericaceae species (KNAPP 1965: 300), the latter being a climax vegetation belt between cloudforests and paramos. LEON's (1946) "monte fresco" term includes this type, too. (An elfin thicket is illustrated by the photograph in Fig. 33 as "monte fresco".) This vegetation type is much drier than the shrubwoods of the cloudy zone, partly because it is above condensation belt and partly because water is rapidly drained from the steep rocky surface. This is why many herbaceous leaf-succulents and spinose shrubs are found here. Within this nodum two associations may be recognized. The first is a dense bush composed of 1.5–2 m high microphyllous and nanophyllous evergreen shrubs (*Ilici–Myricetum cacuminis*) and is characterized by *Ilex turquinensis, I. nunezii, Peratanthe cubensis, Myrica cacuminis, Lobelia cacuminis*,

Fig. 4. Elfin thicket, a humid evergreen shrubland on the Cuba Peak (Sierra Maestra) at 1850 m (Photo: A. Borhidi)

Eupatorium (*Ageratina*) *paucibracteatum*, *Vernonia parvuliceps*, *V. praestans* ssp. *cacuminis*, *Weinmannia pinnata*, *Persea similis*, *Lyonia calycosa*, *Torralbasia cuneifolia*, and *Viburnum villosum*, etc. The other association, *Agavo–Mitracarpetum acunae*, is a 50–100 cm high evergreen thicket on steep rocky slopes. This is rich in lianes, subshrubs and orchids rooted in the moss carpet. Prominent characteristic species are emergent agaves (*Agave pendentata*) and many small epiphytic orchids living on the ground here (*Pleurothallis gelida*, *P. obliquipetala*, *P. wrightii*, *P. testifolia*, *P. parvula*, *P. velaticaulis*, *Lepanthes turquinoensis*, *L. pergracilis*, *L. blepharantha*, *Lepanthopsis microlepanthes*). Typical members of the shrub layer are the dominant *Ilex turquiensis*, *I. nannophylla*, *Mitracarpus acunae*, *Cassia turquinae*, *Micromeria bucheri*, *Juniperus saxicola*, *Schoepfia stenophylla*, *Vernonia praestans* ssp. *cacuminis*, *Eugenia maestrensis*, and *E. lomensis*. Of the herbs *Chaptalia turquinensis*, *Pilea micromeriifolia*, *Peperomia galioides*, *P. grisebachiana*, and *Begonia lomensis* are to be mentioned. *Chusquea abietifolia* and *Arthrostylidium multispicatum* are dominant lianes densely entangling the vegetation.

SEASONAL EVERGREEN FORESTS

Seasonal evergreen forests or seasonal rainforests

Many authors do not make a distinction between the important tropical seasonal forests and the true rainforests. For example, the *Spondias–Oreodoxa* association of Ciferri (1936: 222), thought to be true tropical rainforest, is in fact a seasonal lowland rainforest. The "forêt ombrophile tropicale" category used by many French researchers comprises seasonal forest formation. Others, e.g. Walter (1962) disagree only with the adjective "seasonal". Our vegetation type is identical with the "seasonal evergreen forest" of Beard (1944), although that type may be more broadly interpreted. The Jamaican equivalent is the "wet limestone forest" (Asprey and Robbins 1953). In Puerto Rico seasonal evergreen forest is called "lowland rain forest" by Dansereau (1966: 20). He uses "seasonal evergreen forest" for a drier formation than Beard's community of the same name. Dansereau's seasonal evergreen forest should be called a semideciduous forest. Knapp (1965: 263–264) uses the term "semideci-

duous moist forest", which is obviously unacceptable as these forests are actually evergreen. The reason for this nomenclatural confusion is that these forests are transitional between the rainforests and semi-deciduous forests. They are closer to the rainforests in structure (number of strata, richness in epiphytes). However, the presence of deciduous emergents, the highly developed liane stratum and the absence of shade-tolerant epiphytes and epiphylls emphasize their similarity to the semi-deciduous forests. In the Antilles this formation, the climax type in extensive areas, can be clearly distinguished from both the rainforests and the semi-deciduous forests.

Lowland seasonal evergreen forests

This vegetational zone formerly occupied the most extensive areas in the island and is still widespread in Cuba. It is a climax formation in tropical seasonal climate with 3–5 dry months and 1200–1600 mm annual precipitation, it occurs on calcareous, ferrallitic, and deep red ferrallitic soils. On shallower ferrallitic soils it may develop only if there are not more than one or two dry months a year, as longer dry seasons are more favourable for semi-deciduous forests. This forest zone is the most suitable for tropical agriculture. Consequently, undisturbed stands are hardly found anywhere in Cuba. Their probable physiognomy is reconstructed from semi-cultivated fragments, and from studying standard trees of agricultural savannas and the shade trees of abandoned lowland coffee plantations. Two canopy levels, both evergreen, are recognized. The upper is more open and 20–25 m high, the lower is closed and 8–15 m high. Typically there are emergent specimens of the deciduous *Ceiba pentandra* which may be as tall as 30–40 m. Elements of the upper canopy layer are *Roystonia regia*, *Guazuma ulmifolia*, *Bucida buceras*, *Mastichodendron foetidissimum*, *Lonchocarpus domingensis*, *L. latifolius*, *Luehea speciosa*, *Chlorophora tinctoria*, *Cecropia peltata*, *Cordia collococca*, *C. gerascanthus*, *Ficus* species, and many microphyllous trees, such as *Pithecellobium cubense*, *Samanea saman*, and *Peltophorum adnatum*. In the lower canopy *Oxandra lanceolata*, *Andira inermis*, *Gymnanthes lucida*, *Crescentia cujete* are characteristic species. Drought-tolerant epiphytes (*Tillandsia fasciculata*, *T. recurvata*, *T. valenzuelana*, *T. polystachya*, *T. tenuifolia*) and lianes (*Philodendron lacerum*, *Ph. krebsii*, *Ph. clementis*, *Hylocereus undatus*, *Pithecoctenium echinatum*) are commonly found on tall trees. The royal palm-cotton tree-Samanea agricultural savannas widespread in the northern Caribbean are derived from these forests by logging, burning and grazing.

Submontane seasonal evergreen forests (*Oxandro-Dipholietum*)

These are forest formations in the submontane zone from 200 m to 800 m in altitude. They have a seasonal climate with one to three dry months and an annual rainfall averaging 1400–1800 mm. These forests correspond to LEÓN's (1946) "yayales" formation. They are similar to the lowland seasonal rainforests in structure but the megatherm trees differ. *Ceiba pentandra*, *Samanea saman*, *Guazuma ulmifolia*, and *Zanthoxylum elephantiasis* are absent. Of the emergents *Dipholis jubilla* occurs in the Oriente whereas *Dipholis salicifolia* or *Cedrela mexicana* specimens are found elsewhere. These forests have different composition in the different mountains. In the stands sampled in Sierra Maestra *Dipholis jubilla* is the only buttressed emergent tree. *Calophyllum calaba*, *Zizyphus rhodoxylon*, *Ficus berteroi*, *Zanthoxylum martinicense*, *Z. cubense*, *Didymopanax morototoni*, *Sapium jamaicense*, *Faramea occidentalis*, *Cedrela mexicana*, *Guarea guidonia*, *Cupania glabra*, *C. americana*, and *Roystonea regia* are characteristic of the closed upper canopy, and *Oxandra lanceolata*, *O. laurifolia*, *Chrysophyllum*

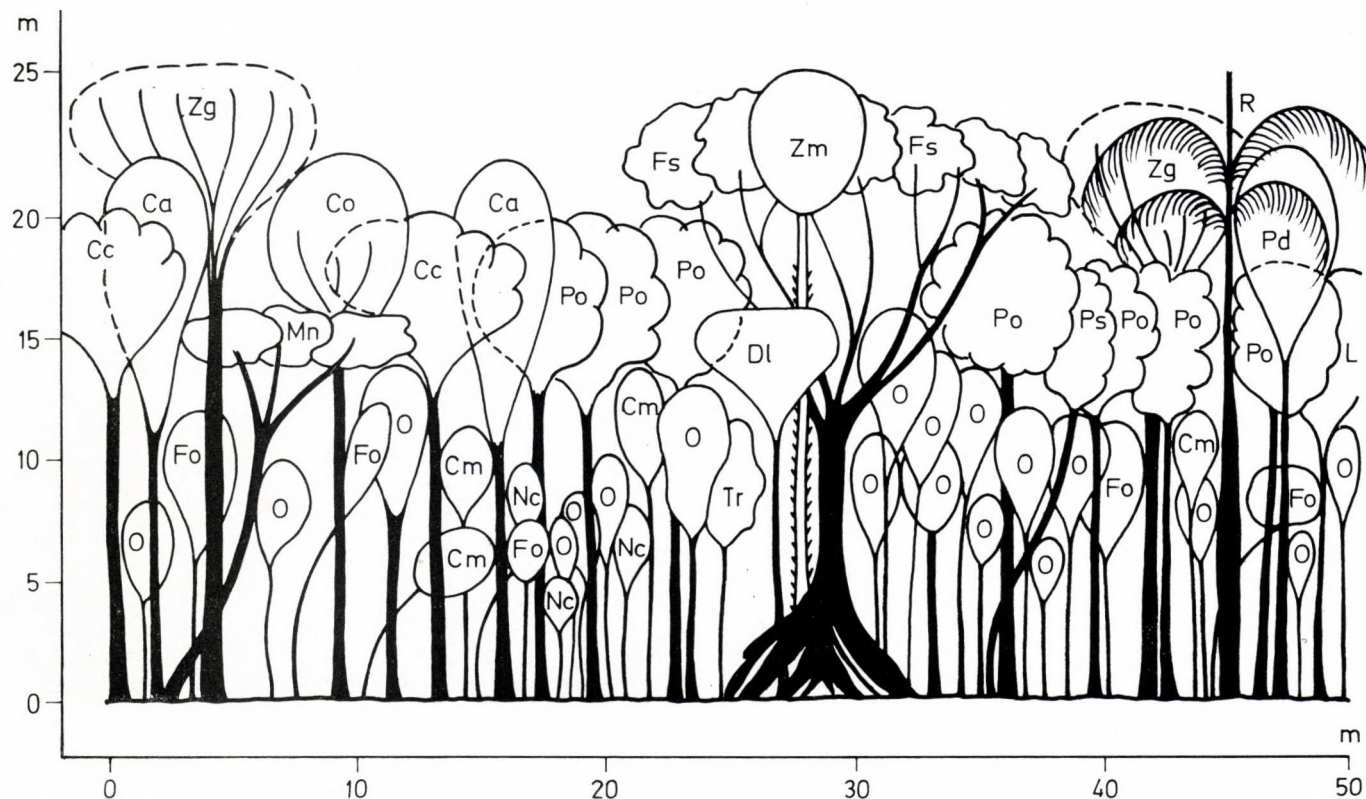



Fig. 5. Perfile of a seasonal evergreen forest stand in the Sierra de la Güira Mountains (Pinar del Rio Province) at 350 m above the sea level (made by A. BORHIDI and R. CAPOTE, 1975; original) — Ca = *Calophyllum antillanum;* Cc = *Cordia collococca;* Co = *Cedrela odorata;* Cm = *Cupania macrophylla;* Dl = *Drypetes lateriflora;* Fo = *Faramea occidentalis;* Fs = *Ficus subscabrida;* Lj = *Licaria jamaicensis,* Mn = *Margaritaria nobilis,* Nc = *Nectandra coriacea;* O = *Oxandra lanceolata;* Pd = *Pouteria dictyoneura;* Po = *Prunus occidentalis;* Ps = *Pseudolmedia spuria;* R = *Roystonea regia;* Tr = *Trophis racemosa;* Zg = *Zuelania guidonia;* Zm = *Zanthoxylum martinicense*

argenteum, *Dendropanax arboreus*, *Lonchocarpus latifolius*, *Sloanea amygdalina*, *Wallenia laurifolia*, and *Gymnanthes lucida*, etc., occur in the lower stratum. The herb layer is dominated by terrestrial ferns from the genera *Dryopteris*, *Asplenium*, *Adiantum*, *Tectaria*, *Diplazium*, and *Dennstaedtia*. These ferns, the mesophytic orchids of the epiphyte layer (mostly *Epidendrum*, *Encyclia* and *Oncidium* species) and the mesophilous lianes allow a clear distinction to be made between seasonal rainforests and semi-deciduous forests. The difference is even more emphasized by the presence of epiphyllous lichens and bryophytes growing on trunks

SEMI-DECIDUOUS FORESTS

Semi-deciduous mesophytic forests (*Oxandro-Burseretalia*)

These are natural forests which are widespread especially in the lowlands and hills of western and central Cuba where the annual rainfall is 1200–1700 mm and the dry seasons are of three to six months duration. In the Antilles this vegetation type is generally distributed. CIFERRI's (1936: 201) *Catalpa-Swietenia* association and the "Hammock forests" of Florida (KNAPP 1965) are examples, such communities have been described by DANSEREAU (1966) from Puerto Rico, and by BEARD (1949) and STOFFERS (1956) from the Lesser Antilles. Two canopy layers occur, the height of the tallest trees ranges from 18 to 25 m. In the upper canopy layer the cover of deciduous trees is not more than two-thirds of the total cover. The 6–12 m high second stratum is composed exclusively of evergreens, partly of sclerophyllous ones. Deciduous giant trees (*Ceiba pentandra*, *Bombacopsis cubensis*) may also be present but are sparsely distributed in any case. Prominent elements of the upper canopy layer are *Ficus*

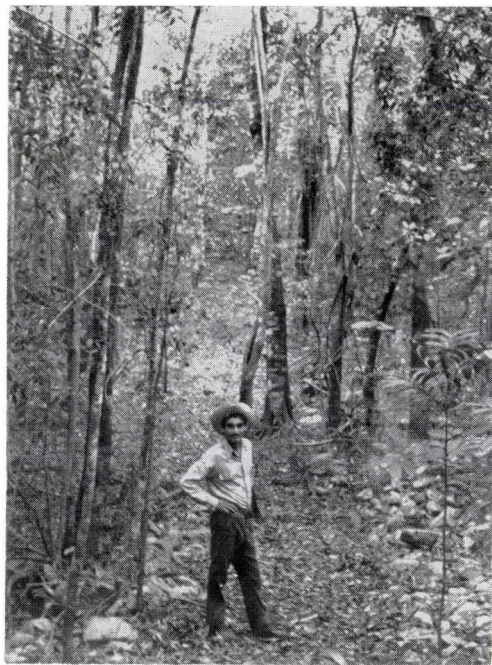



Fig. 6. Seasonal evergreen forest in the Rosario Mountains, (Photo: A. BORHIDI)

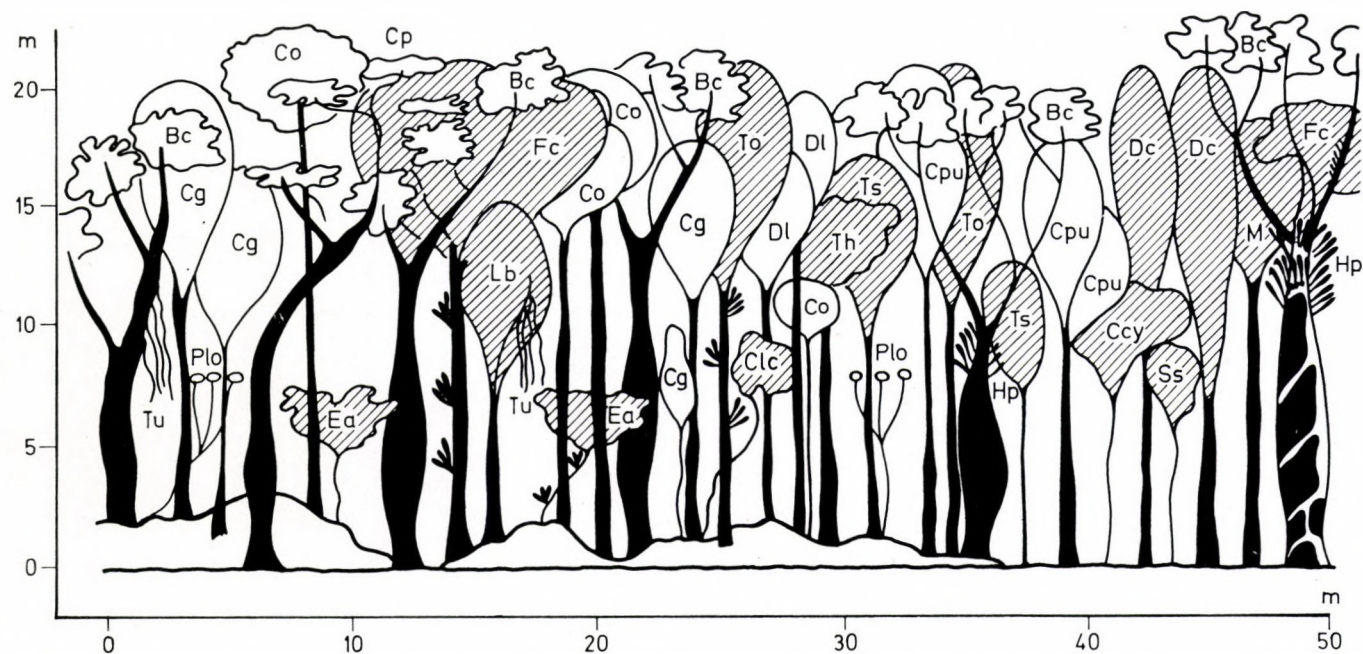



Fig. 7. Perfile of a semideciduous limestone forest in the Guanahacabibes Peninsule, El Veral Nature Conservation Area. Made by A. Borhidi and R. Capote 1974; original — Bc = *Bombacopsis cubensis;* Ccy = *Capparis cynophallophora;* Cg = *Cordia gerascanthus;* Co = *Cedrela odorata;* Cp = *Ceiba pentandra;* Cpu = *Catalpa punctata;* Dc = *Diospyrus crassinervis;* Dl = *Drypetes lateriflora;* Ea = *Eugenia axillaris;* Fc = *Ficus crassinervis;* Lb = *Linociera bumelioides;* Plo = *Plumeria obtusa;* Th = *Trichilia hirta;* To = *Torrubia obtusata;* Ts = *Tabebuia shaferi;* Clc = *Clerodendron calcicola;* Hp = *Hohenbergia penduliflora;* Ss = *Savia sessiliflora;* Tu = *Tillandsia usneoides*

crassinervis, Cedrela mexicana, Andira inermis, Bursera simaruba, Mastichodendron foetidissimum, Pithecellobium cubense, Zanthoxylum elephantiasis, Catalpa punctata, Tabebuia shaferi, Zuelania guidonia, Casasia calophylla, and *Casearia hirsuta.* In the second layer *Amyris balsamifera, A. elemifera, Trichilia hirta, Picramnia pentandra, Adelia ricinella, Diospyros crassinervis, Krugiodendron ferreum, Ateleia cubensis, Eugenia axillaris, E. rhombea, E. maleolens, Canella winterana, Allophylus cominia, Savia sessiliflora, Cordia gerascanthus,* and *Gymnanthes lucida* are common. The epiphyte level is fragmented, only the emergent trees possess vast numbers of epiphytic plants, especially drought-resistant *Tillandsia* species. Many lianes, with xerophytic microphylls occur, e.g. *Pisonia aculeata, Celtis iguanea, Solandra longifloria, Chiococca alba, Cissus sicyoides, C. formosa, Canavalia ekmanii, Dalechampia scandens, Serjania diversifolia, Abrus precatorius, Securidaca elliptica, Clematis dioica, Passiflora suberosa, P. multiflora, Bauhinia divaricata, Pithecoctenium echinatum, Stegnosperma scandens, Platygyne hexandra,* and *Smilax havanensis,* etc. The herb layer is poor or even completely lacking, so are the shade-tolerant ferns. Three closely related associations coming from three different regions of Cuba were studied. The *Pseudobombaci-Burseretum* community in the Guanahacabibes peninsula is characterized by emergent giant trees and Mexican elements, the *Coccolobeto-Burseretum* association of Isla de Pinos and the Zapata peninsula has many microphyllous coastal plants, and the *Zanthoxylo-Burseretum* community on the hills in Las Villas and Camagüey has several rainforest trees.

Semi-deciduous xerophytic forests

These are relatively low (12–15 m) forests with a single canopy layer, found in the lowlands and hills of the eastern part of central Cuba, on sandy or rocky, acidic or neutral soils that are poor in nutrients. Annual precipitation is 800–1200 mm, the seasonal climate has 5–6 dry months. The canopy level is up to 80% closed and is partly composed of deciduous trees. Characteristic trees are, for example, *Bursera simaruba, Cordia gerascanthus, C. collococca, C. nitida, Phyllostylon brasiliensis, Gossypiospermum praecox, Manilkara jaimiqui* ssp. *wrightiana, Maytenus buxifolia, Belairia spinosa, Pisonia rotundata, Ficus laevigata, Eugenia*

Fig. 8. Semi-deciduous littoral forest in the Zapata Peninsule, near to Playa Girón (Photo: A. BORHIDI)

maleolens, Hypelate trifoliata, Piscidia piscipula, Ateleia apetala, Canella winterana, Diospyros halesioides, Tabebuia anisophylla, T. trachycarpa, Carpodiptera cubensis, Copernicia baileyana C. textilis, and *C. sueroana.* The shrub layer consists mainly of spiny sclerophylls, e.g. *Brya ebenus* s.l., *Malpighia, Randia,* and *Oplonia* species. Natural stands are rare, their physiognomy is similar to the cerradao vegetation of the cerrado forest zone in Brazil, as described by EITEN (1972). As a result of burning and grazing most stands have been replaced by secondary savannas dominated by either *Copernicia* palms or deciduous trees.

Tropical karstic forests

These are extremely diverse forests on shallow humic-carbonated rendzina or bare rocks of deeply eroded mountains and solitary cliffs consisting mainly of hard Jurassic and Triassic limestones. Usually a single, 5–10 m high open canopy layer composed mainly of deciduous trees occurs. In Cuba this formation is most similar to the dry deciduous forests. Thanks to the favourable light conditions, the usually epiphytic plants live on the ground forming a closed herb layer on rocks where water balance is just as poor as on the trunk or at canopy level. In extreme habitats which become dry and hot very quickly, succulent agaves, epiphytic, columnar and liane-like cacti (*Rhipsalis, Leptocereus, Selenicereus, Pilosocereus*), and trees with barrel-shaped trunks capable of water storing (*Gaussia, Bombacopsis*) are found. The thickness of soils, if any, is extremely uneven due to erosion and soil accumulation caused by geomorphological formations. Therefore, the vegetation itself is also of mosaic structure. LÖTSCHERT (1958) takes the view that no associations can be distinguished in the mogotes. Of course, associations in the sense applied to the temperate zone, especially to central Europe, cannot be recognized in the tropical vegetation if characterized by a multitude of dominant species (tropical coniferous forests, mangroves, littoral communities and savannas are usually exceptions), but I think it — possible to define associations. Under favourable conditions seven well-defined vegetational noda may be distinguished in the mogotes: herbaceous communities of the insolated (1) and those of shaded (2) crevices, shrub dominated (3) and bromeliad dominated (4) mogote forests, semideciduous forests on rocks (5) and at the foot of hills (6), and seasonal rainforests in the gorges (7). The first four communities comprise the "mogote complex" in the wider sense. This complex is hard to subdivide for technical reasons. The shrub and bromeliad dominated mogote forests can be treated as "mogote forests" in narrower sense. The mogote forests of the bromeliad type are absent from the soft limestone formations (e.g. Las Villas, Oriente) where only the shrubby variant may develop. The mogote forests have two evolutionary centres with completely different floras, the older in western Cuba (*Bombacopsis-Thrinacetalia*), the another in the central and eastern part of the island (*Tabebuio-Coccothrinacetalia*). Both vegetation types served as a basis for the flora development on the rocky coasts. Most of the mogotes of eastern Cuba were themselves located on the coastal zone in the Tertiary. Therefore, the connection between the flora of these mogotes and the recent coastal zone had been stronger than that between the coast and the mogotes of Sierra de los Organos that were separated from each other by slatey outcrops.

Species rich karstic forests of western Cuba (Spathelio-Gaussion)

These are open forests composed of 5–8 m high, mostly deciduous trees on the steep slopes and the top of the karstic mountains in Sierra de los Organos. Characteristic are *Bombacopsis cubensis* and *Gaussia princeps* with barrel-like trunks, and the tree fern-shaped *Spathelia brittonii, Thrinax morrisii, Ekmanianthe actinophylla, Omphalea hypoleuca, Bourreria poly-*

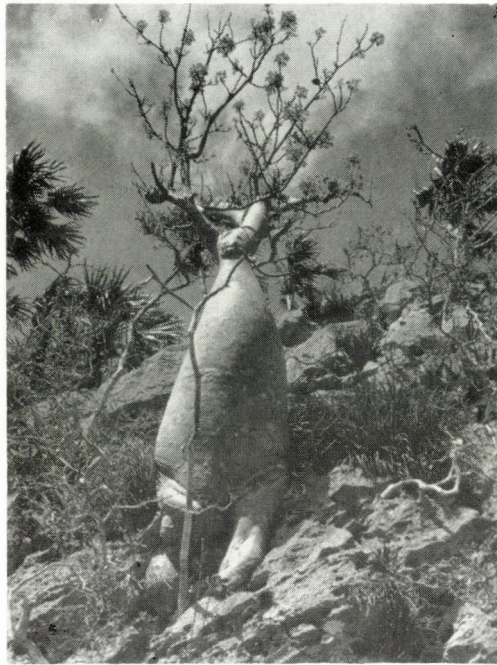



Fig. 9. Tropical karstic forest in the Organos Mountains (Pinar del Rio Province) with barrel shaped *Bombacopsis cubensis* and *Thrinax morrisii* palms, *Plumeria* and *Erythrina cubensis* (Photo: A. BORHIDI)

neura, *Microcycas calocoma*, *Plumeria emarginata*, *Colubrina elliptica*, *Citharexylum caudatum*, *Erythrina cubensis*, *Sapium leucogynum*, *Trichilia havanensis*, and *Zanthoxylum pimpinelloides*. In the bromeliad dominated variant (*Vrieseo-Bombacopsidetum*) *Hohenbergia penduliflora*, *Vriesea dissitiflora* and twelve *Tillandsia* species are typical. Dominant species of the shrubby variant are *Ceratopyxis verbenacea*, *Eugenia galeata*, *Psidium vicentium*, *Oplonia purpurascens*, *Annona cascarilloides*, *Malpighia roigiana*, *Guettarda calcicola*, etc. Of the succulents *Agave tubulata*, *Leptocereus assurgens*, and *Selenicereus grandiflorus* are worth mentioning. Lianes, such as *Siemensia pendula*, *Philodendron urbanianum*, and *Cuervea integrifolia*, and chasmophytes, e.g. *Gesneria celsioides*, *Rhytidophyllum rupincola*, *Anthurium venosum*, and *Peperomia verticillata* are also common. The endemic taxa account for 40% of the total of the presence scores in the data, suggesting that among the limestone formations of Cuba these forests are the richest in endemics.

Species poor karstic forests of western Cuba (Thrinacion morrisii)

These forests are found in the limestone karsts originated from the Cretaceous and the Eocene in the provinces of Habana and Matanzas, between 200 and 300 m altitude, in a seasonal climate of one to four dry months and 1200–1600 mm rainfall per year. In these rocks, that are softer than the Jurassic limestone of Sierra de los Organos, the biologically induced karstification process is intensive so these karstic forests are poorer in chasmophytes, most of those being replaced by mesophytic and hydrophytic elements of canyon forests

(*Peperomia*, *Piliea*, *Rhytidophyllum* and fern species). Most typical of these forests is the *Bombacopsi-Thrinacetum morrisii* association, which was studied in the mogotes of Jaruco. *Thrinax punctulata* is dominant, its 5–6 m high canopy layer is barely broken by emergent individuals of *Bombacopsis cubensis*. An addition element characteristic of the Viñales mogotes but also present here is *Agave tubulata*. The others are replaced by more common calciphilous species, such as *Celtis trinervia*, *Ery:hroxylum areolatum*, *Ficus jacquinifolia*, *F. aurea*, *Casearia guianensis*, *C. hirsuta*, *Hamelia patens*, *Bocconia frutescens*, *Piper umbellatum*, *Trichilia havanensis*, and *Cordia globosa*. The occurrence of the spiny shrub *Leucocroton microphyllus* is typical of dry habitats. *Rhytidophyllum exsertum* occurs in shaded crevices in rocks. The community is strikingly poor in epiphytes.

Karstic forests of eastern Cuba (Tabebuio-Coccothrinacion)

Isolated stands of different size extend from the limestone cliffs of Las Villas as far as the Baracoa area, including the karstic block mountains of Camagüey and the extensive mogote zone of Nipe and Sierra Maestra. They are different from the western mogotes in four respects: 1. Trees with barrel-like trunks are absent, 2. *Thrinax* palm is replaced by *Hemithrinax* and *Coccothrinax* species, 3. Columnar cacti are customarily found, and 4. deciduous elements are less abundant, being replaced by evergreen sclerophyllous trees and shrubs. The floristic composition differs with the various mountain areas. The isolated mogote floras of Las Villas and Camagüey are poor in species. The most developed stands, that are repeatedly found are representatives of the association *Coccothrinaci-Tabebuietum bibracteolatae*. They were examined in the northern karstic area of Sierra Maestra. This is in fact a shrubwood with loose canopy layer and dominated by microphyllous evergreen trees, epiphytes and lianes. On the rims columnar cacti (*Pilocereus brooksianus*) and agaves occur. Characteristic trees are *Coccothrinax elegans*, *Tabebuia bibracteolata*, *Alvaradoa arborescens*, *Ficus jacquinifolia*, *Plumeria ekmanii*, and *P. filifolia*, *Swietenia mahagoni*, *Pithecellobium cubense*, *Zanthoxylum spinosum*, *Colubrina elliptica*, *Catalpa brevipes*, *Hyperbaena cubensis*, *Helietta glaucescens*, *Thouinia trifoliata*, *Cordia alliodora*, *Dendropanax arboreus*, *Savia erythroxyloides*, and *Strempeliopsis strempelioides*. In the shrub layer *Bernardia dichotoma*, *Eugenia maleolens* and *Forsteronia corymbosa* are dominant. Additional species are several local endemics (*Neobracea susannina*, *Malpighia acunana*, *Rhytidophyllum mogoticola*, *Lunania cubensis*, and more than 20 lianes (e.g. *Marcgravia rectiflora*, *Byttneria microphylla*, *Tournefortia volubilis*, *Selenicereus grandiflorus*, *S. urbanianus*, *Serjania diversifolia*, *S. crassinervis*, *Philodendron lacerum*, *Ph. krebsii*, *Cissampelos pareira*, and *Anguria pedata*).

Montane karstic forests (Tabebuio-Garryetum)

These occur in the karsts situated in the montane rainforest zone or at its margin. Annual mean temperature is 19–21 °C, average annual precipitation is 2000 mm and evenly distributed. A single stand was examined in Pico Potrerillo, Sierra Escambray, at an altitude between 850 and 930 m. It is characterized by a 6–8 m high loose canopy layer composed of drought-tolerant deciduous trees. A highly dense, 2–3 m high shrub layer containing many montane rainforest elements occurs beneath the trees. The rocks, logs and trunks are covered with rich moss assemblages, many rainforest epiphytes (*Pleurothallis* spp., *Lepanthes* spp., *Guzmania monostachya*, *G. lingulata*, *Catopsis nitida*), and hygrophilous herbs (*Begonia*, *Peperomia*, *Pilea*, *ferns*). Characteristic elements are *Thouinia clarensis*, *Garrya fadyenii*, *Berberis tenuifolia*, *Dendropanax arboreus*, *Coccothrinax trinitensis*, *Terminalia neglecta* and *Ocotea*

floribunda in the canopy layer, and *Ilex clementis*, *Tabebuia sauvallei*, *Bernardia dichotoma*, *Savia sessiliflora*, *Citharexylum matheanum*, *Erythroxylon clarense*, *Karwinskia potrerilloana*, *Sapium leucogynum*, and *Psychotria martii* in the shrub layer.

DRY FORESTS AND SHRUBWOODS

These are the forest communities of arid zones, but are also found elsewhere if edaphic conditions are poor (shallow soils). In the arid zones the climate is seasonal with one dry season in the winter or with two dry seasons; the number of dry months is five to nine, annual precipitation ranges from 600 to 1200 mm. These formations may also develop on serpentines or in the coastal zone even though climate is more humid in these places. Dominant are the microphyllous and nanophyllous trees and shrubs, most of them being sclerophyllous evergreens or having compound leaves (e.g. Mimosaceae and Caesalpiniaceae). Spinose elements are common, reaching as much as 33% of the presence scores, especially on serpentine. Epiphytes, mosses and cacti are very poorly represented. The liane flora, however, is rich with drought-resistant herbaceous life forms predominating.

Dry evergreen forests (*Eugenio-Metopietalia toxiferi*)

10–18 m high forests with one or two canopy layers. They occur on limestone rendzina and humic carbonate soils or shallow red ferrallitic soils, usually close to the coasts. These forests correspond to the "dry evergreen forests" and "littoral forests" described by BEARD (1944), and to the "dry limestone scrub forests" of ASPREY and ROBBINS (op. cit.). CIFERRI's "foresta subxerofitica" associations also belong to this group. The dry evergreen forests are widespread along the rocky coasts of Cuba and even in the higher terraces looking on to the sea in Oriente, especially at Cabo Cruz and Maisi. The height of trees if 15–18 m if two canopy strata occur, or 8–12 m in a single layered canopy. Characteristic constituents are the Mimosaceae and Caesalpiniaceae which dominate the canopy layer, and other sclerophyllous trees. The most widespread community is the 12–18 m high *Lysilomo-Burseretum simarubae* association, the climax stage of the successional sere on littoral rocks. In structure, dry evergreen forest is similar to the semi-deciduous forests. Depending on soil depth and human impact the structure and floristic composition of the stands are highly variable. Constant and common species of the canopy layer are *Bursera simaruba*, *Lysiloma bahamensis*, *Thrinax radiata*, *Ficus aurea*, *Capparis cynophallophora*, *C. flexuosa*, *Coccoloba diversifolia*, *Chrysophyllum oliviforme*, *Tabernaemontana amblyocarpa*, *Caesalpinia vesicaria*, *C. bahamensis*, *Ateleia gummifera*, *Pithecellobium lentiscifolium*, *Carpodiptera cubensis*, *Hypelate trifoliata*, and *Hippomane mancinella*. Prominent elements of the shrub layer and the lower canopy level are *Amyris balsamifera*, *Gymnanthes lucida*, *Eugenia maleolens*, *E. axillaris*, *Bourreria succulenta*, *Croton lucidus*, *Cordia globosa* ssp. *humilis*, *Plumeria emarginata*, *Lantana involucrata*, *Exostema caribaeum*, *Erythroxylon areolatum*, *E. rotundifolium*, *Caesalpinia pauciflora*, *Solanum bahamense*, *Adelia ricinella*, and *Schaefferia frutescens*. Of the 25 liane species *Caesalpinia crista*, *Pisonia aculeata*, *Morinda royoc*, *Solandra longiflora*, *Smilax havanensis*, and *Jacquemontia jamaicensis* are worth mentioning. In limestone areas covered with shallow and rocky soils the forest canopy is uneven rather open and 6–10 m high. An example is the *Krugiodendro-Drypetetum* association described by CIFERRI (1936) from Hispaniola, which is similar to the communities found at Maisi and in the Guanahacabibes peninsula. The *Swietenio-Metopietum brownei* association is of similar distribution to the former community and it is found in the southern part of Isla de Pinos, in the Zapata peninsula and the nearby southern

Fig. 10. Dry littoral evergreen forest in the Zapata Peninsule. Perfile made by A. BORHIDI, E. DEL RISCO and RAMONA OVIEDO, 1975; original; — Ar = *Adelia ricinella;* Bs = *Bursera simaruba;* Bsc = *Bourreria succulenta;* Ccy = *Capparis cynophallophora;* Cf = *Capparis flexuosa;* Cr = *Colubrina reclinata;* Csc = *Casasia calophylla;* Ec = *Exostema caribaeum;* Em = *Eugenia maleolens;* Er = *Erythroxylum rotundifolium;* Fr = *Forestiera rhamnifolia;* Hm = *Hippomane mancinella;* Hr = *Hyperbaena racemosa;* Ht = *Hypelate trifoliata;* Lb = *Lysiloma bahamense;* Od = *Opuntia dillenii;* Pa = *Peltophorum adnatum;* Pb = *Pilosocereus brooksianus;* Pcr = *Picrodendron macrocarpum;* Ph = *Piscidia havanensis;* Sg = *Selenicereus grandiflorus;* Sm = *Swietenia mahagoni;* Tm = *Tabebuia myrtifolia;* To = *Torrubia obtusata;* Zg = *Zuelania guidonia*

coasts. Characteristic trees are *Swietenia mahagoni, Metopium brownei, Picrodendron macrocarpum, Krugiodendron ferreum, Pithecellobium cubense, Terminalia neglecta, Bucida spinosa Nectandra coriacea, Elaeodendron attenuatum* s.l., *Acacia farnesiana, Peltophorum adnatum, Linociera ligustrina, Belairia ternata, Pseudocarpidium wrightii, Manilkara jacquinii, Capparis* and *Erythroxylon* species, *Gyminda latifolia, Chrysobalanus icaco,* and *Canella winterana.* Of the palms *Coccothrinax litoralis* and *Sabal parviflora* are common the latter occurring in habitats with stagnant water in the summer. The shrub layer is rich in species, the commonest plants being spiny shrubs and lianes, such as *Coccoloba armata, Jacquinia aculeata,* and *J. stenophylla, Malphighia cubensis, Zanthoxylum fagara, Caesalpinia crista, C. bonduc, Leucocroton microphyllus, Comocladia dentata, Randia aculeata, Brya ebenus,* etc. The dry coastal forests of northern and southern Oriente may also be assigned to this vegetation type. These are rich in *Acacia* species (*A. roigii, A. curbeloi* and *A. cupeyensis* between Puerto Padre and Banes; *A. lutea* and *A. seifriziana* at Maisi, and *A. cowellii* at Santiago de Cuba). The floristic composition of these communities is not known exactly, but there is an obvious similarity to the *Phyllostylon-Acacia* and *Acacia-Krugiodendron* associations reported from Hispaniola by Ciferri. The 'thorn scrub' of Asprey and Robbins also overlaps with the dry evergreen forests (*Acacia-Prosopis*).

Dry, thorny limestone shrubwoods (*Lantano-Cordietalia*)

This is the dense vegetation composed of thorny sclerophyllous, small-leaved trees and shrubs occurring on bare rocks of dry limestone terraces and the 'doghtooth' lowland karstic formations. The 2–3 m high shrubs and the emergent individuals or groups of 5–6 m high "rod like" trees form an unpenetrable vegetation mosaic described under various names in the literature. In Cuba these are usually called the 'manigua' or 'manigua costera', the latter used for coastal shrubwoods. (It is noted that 'manigua' is the more correct term in the sylvicultural and geographical usage. It means secondary shrubwood, mainly degraded ones developed after logging in forest communities.) This corresponds to the 'thorn woodland' of Beard. These woodlands are best developed under a climate of two dry seasons with together 7–8 dry months and an average annual precipitation of 600–800 mm. Columnar or tree-like cacti may also occur under a loose canopy layer or intermingled with shrubs in some closed fragments of the community. Cacti, however, are never dominant in this vegetation. Smaller stands of this vegetation type are found in the northern coastal zone of Habana and Matanzas and in southern Matanzas and Las Villas. Extensive unbroken stands occur in Oriente between Puerto Padre and Gibara, and in the southern terraced coast between Cabo Cruz and Maisi. This formation is very rich in species. A number of noda, one gradually transformed to the other, may be defined. Characteristic trees are *Picrodendron macrocarpum, Cordia leucosebestena, Colubrina elliptica, Maytenus buxifolia, Polygala cuneata, Auerodendron cubense, Erithalis fruticosa, Cassia emarginata, Gymnanthes lucida, Pseudocarpidium wrightii, P. avicennoides, P. multidens, Diospyros grisebachii, Spirothecoma spiralis,* and *Thouinia pseudopunctata.* Main elements of the shrub layer are *Croton lucidus, C. rosmarinoides, C. myricifolius, Jacquinia berteroi, J. maisiana, Eugenia cowellii, Exostema spinosum, Grimmeodendron eglandulosum, Polygala guantanamana, Erythroxylon minutifolium, Bellonia spinosa, Pithecellobium hystrix, Calliandra colletioides, Randia spinifex, Oplonia polyece, Tabebuia myrtifolia, T. polymorpha, Cordia globosa, C. pulverulenta, C. brittonii, C. leptoclada, Bunchosia linearifolia, Plumeria* and *Savia* species, *Coccothrinax fragrans, C. munizii, C. microphylla* and *Lantana involucrata.* Of the succulents *Agave underwoodii, Melocactus harlowii, M. borhidii, Harrisia fernowii,* and in some places *Dendrocereus nudiflorus* and *Ritterocereus hystrix* occur. The number of herbs and drought-tolerant epiphytes (e.g. *Tillandsia circinnata, T. balbisiana, T. recurvata, T. flexuosa,*

Fig. 11. Dry evergreen littoral thicket in the Maisi Plain (Guantánamo Province) with emergent *Coccothrinax alexandri* palms (Photo: A. BORHIDI)

T. pruinosa) is low. Of the 30 lianes more common are *Mesechites rosea*, *Aristolochia clementis*, *Helicteres semitriloba*, *Stigmaphyllon* spp., *Passiflora santiagana*, *P. cuprea*, *P. suberosa*, *P. multiflora*, *Distictis rhynchocarpa*, *D. gnaphalantha*, *D. lactiflora*, *Gayoides crispum*, *Jacquemontia jamaicensis*, and *Morinda royoc*, etc.

Dry lowland serpentine shrubwoods (*Phyllantho-Neobracetalia valenzuelanae*)

These communities occur on red ferrallitic soils derived from serpentine in several isolated spots from the Cajalbana Hills to the Holguin serpentine area in Oriente. Thec limate is characterized by a single dry season (or two in the east) with 1–2 to 5–6 dry months and annual precipitation averaging 1000–1600 mm a year. Aridity tends to increase towards the east. This vegetation type, called the 'cuabales' in Cuba, corresponds to BEARD's 'dry evergreen scrub forest' or 'scrub woodland', which is a zonal community on limestone with an annual precipitation of 600–1000 mm. It is characterized by a dense, 2–4 m high closed shrub layer, smaller emergent palms, dwarf palms and 4–6 m high microphyllous evergreen trees. Contrary to the limestone shrubwoods, the physiognomy of serpentine scrub woodlans is quite uniform despite the great differences in climate, soil and floristic composition. The proportion of microphylls and spiny elements is even higher than in the limestone formation. The only major difference is the absence of cacti (except of *Melocactus* species) that usually cannot tolerate the high water retention power (osmotic pressure) of soils derived from serpentine. Another structural characteristic of serpentine scrubs is that the stands alternate with small grassy clearings. These can be transformed into dwarf-grass savannas later by human interference and grazing. Common characteristic species of the lowland serpentine scrubs are *Neobracea valenzuelana*, *Phyllanthus orbicularis*, *Annona bullata*, *Rondeletia camarioca*, *Eugenia camarioca*, *Zanthoxylum rolandi*, *Cynanchum ophiticolum*, *Passiflora cubensis*, *Ipomoea carolina* ssp. *ophiticola*, *Tabebuia lepidota*, *Coccothrinax miraguama*, and *Malpighia nummulariifolia*, etc. Two vegetational noda, differing in their past flora development, may be distin-

Fig. 12. Dry thorny serpentine shrubwood in Las Villas Province, near to Santa Clara, with *Agave brittoniana, Erythroxylum minutifolium, Brya ebenus, Bursera angustata* (Photo: A. BORHIDI)

guished. The serpentine scrubs of western central Cuba are included in the *Coccothrinaci-Tabebuion lepidotae* alliance containing *Coccothrinax miraguama* ssp. *roseocarpa, Ottoschmidtia dorsiventralis, Leucocroton havanensis, Anemia cajalbanica*, and *Eugenia sauvallei*, etc. Those of the eastern part of central Cuba belong to the *Guettardo-Jacarandion cowellii* nodum which includes three local associations, *Rondeletio-Guettardetum clarensis* in Las Villas, *Copernicio-Tabebuietum trachycarpae* in Camagüey, and *Acacio belairioidi-Spirotecometum holguinensis* and related communities at Holguin, all these occur solely in sites not disturbed by grazing.

Semi-dry lowland serpentine shrublands (*Ariadno–Phyllanthetalia*)

Evergreen shrublands developed almost exclusively on the ferritic latosols of the coastal zone north of the Moa Mts, and on the semihumid serpentine rendzinas in the hilly and lovermontane zones of the Sagüa-Baracoa range. Precipitation averages 1400–1900 mm a year, one or two dry months occur in the spring or early summer. These communities are rather similar to the dry lowland serpentine scrubwoods in physiognomy. However, while the latter are characterized by equal proportions of microphylls and nanophylls, more than 30% of spiny plants and the occurrence of grassy clearings, in the semidry lowland serpentine scrubwoodland microphylls are dominant, the percentage of spiny species is hardly over 10%, and no clearings are present. The ancient endemic flora has originated from Moa, and moved along the coast in both direction. In the dry vegetation type the proportion of endemics reaches 35–45%, in the semidry type endemics account for as much as 75–85% of the flora. In Cuba this formation is the richest in endemics. Main constituents are several species of small trees and shrubs. Common or abundant elements are *Hemithrinax savannarum, H. rivularis, Acrosynanthus minor, Tabebuia linearis, Antirhea abbreviata, A. orbicularis, Phyllanthus comosus, P. chryseus, Purdiaea velutina, Shaferocharis multiflora, S. villosa, Kodalyodendron cubense, Ceuthocarpus involucratus, Exostema purpureum, Neobracea valenzuelana, Spirotecoma apiculata, Jacaranda arborea, Coccoloba shaferi, C. nipensis, C. acuna, Cassia bucherae, Byrsonima bucheri, Suberanthus stellatus, Casasia jacquinioides, C. nigrescens* ssp. *moaensis, Dipholis cubensis, Moacroton leonis, Pachyanthus moaensis*, and *Miconia javorkaeana* (*Graffenrieda*

cordifolia). In the herb layer *Paepalanthus brittonii*, *Machaerina cubensis* and *Rhynchospora* species are found. A special feature of this plant community is that only very few lianes and epiphytes are present. This fact also emphasizes the difference between the dry and semi-dry lowland serpentine shrubwoods.

SEMI-DESERT VEGETATION

Semi-desert cactus scrubs (*Consoleo-Ritterocereion hystricis*)

The cactus scrubs form an unbroken strech along the coast from the Guantanamo Bay to Imias. From Imias to Maisi smaller fragments occur, especially on the sand deposits of the coastal areas. The small trees and shrubs constitute an open vegetation. Succulents, mainly cacti, are codominant or even dominant in both the shrub and canopy layers. This vegetation type is identical with BEARD's 'cactus scrub', the 'cactus-thron scrub' described by ASPREY and ROBBINS, and partly with CIFERRI's 'foresta iperxerofitica'. According to KNAPP (1964, 1965) and HUECK (1966), HUECK and SEIBERT (1972) these scrubs belong to the semi-desert formations and constitute an integral part of coastal semi-deserts in the Caribbean. Several geographically separated associations occur depending on whether the soil is rocky or sandy and on the duration of dry periods. On sandy soils *Ritterocereus hystrix*, *Opuntia dillenii*, *O. militaris*, *Cylindropuntia hystrix* and *Rhodocactus cubensis* are dominant, the sparse herb layer is composed of grasses. Most of the sporadically distributed trees and shrubs are members of the families Caesalpiniaceae and Capparidaceae, e.g. *Caesalpinia*

Fig. 13. Cactus scrub in the South-East coastal belt of Cuba, near to Baitiquiri, with *Agave albescens*, *Pilosocereus brooksianus*, *Colubrina elliptica*, *Oplonia polyece* (Photo: A. BORHIDI)

pinnata, *C. pauciflora*, *Capparis flexuosa*, *C. cynophallophora*, and also *Guajacum officinale*. Dominant species of rocky habitats are *Consolea macracantha*, *Dendrocereus nudiflorus*, *Pilosocereus brooksianus*, *Harrisia fernowii*, *Agave albescens*, and *Melocactus acunae*, the latter two in the herb layer. The shrub flora is very rich, in addition to those mentioned above the *Jacquinia*, *Gochnatia*, *Cordia*, *Guettarda*, and *Lantana* species, and emergent *Coccothrinax* palms (*C. hiorami*, *C. munizii*, *C. alexandri*) are abundant.

CONIFEROUS FORESTS

The primary production and complexity of coniferous forests is lower than those of the climax forests expected under the given climatic conditions. They occur only on nutrient poor acidic soils, either on quartz sands, slates and sandstones as subclimax communities, or as paraclimax communities on ferritic soils. The geographical range of coniferous forests is bipolar, being restricted to the eastern and western ends of the island, where, at the same time, they are the dominant vegetation type.

Pinus tropicalis pine woodland on sands (*Acoelorrhapho–Pinion tropicalis*)

This type is found in the western coast of Isla de Pinos, in a narrow strip north of the Lanier Swamp, in the Guanahacabibes peninsula and the southern plains of Pinar del Rio. The soil is light gray quartz sand with low nutrient content and marked seasonal fluctuation of moisture. The natural pine forests, 'clear pine forests', had a loose canopy layer. As a result of logging they have been replaced by 'pine woodlands' with an even looser canopy (less than 30%), or by scrub and savannas. Contrary to the general view, expressed in BEARD (1953) following the soil surveys of BENNETT and ALLISON (1928) and other sources, the original vegetation was by no means a sort of pine savanna (cf. SAMEK, 1969). SAMEK distinguishes between two vicarious associations: the *Eragrosti cubensi-Pinetum tropicalis* community (ined.) in Pinar del Rio, and the *Paepalantho seslerioidi-Pinetum* association in Isla de Pinos. Characteristic elements of the canopy layer of both types are *Pinus tropicalis*, *Colpothrinax wrightii*, *Acoelorraphe wrightii*, *Tabebuia lepidophylla*, *Chaetolepis cubensis*, *Byrsonia crassifolia*, *B. wrightiana*. In the latter association *Paepalanthus seslerioides*, *Phyllanthus selbyi*, *Syngonanthus insularis*, *Cladium jamaicense*, *Panicum longiligulatum*, *Kalmiella aggregata*, *K. simulata*, *Pachyanthus longifolius*, *Xyris longibracteata*, and *Lyonia vaccinioides* are typical. The canopy layer of both associations is closed up to 10–30%, the cover of shrub is similar. The herbs may cover as much as 40–100% of the ground, and some sparse lichen assemblages also occur.

Pinus caribaea and mixed oak-pine forests on slaty rocks (*Pachyantho–Pinion* and *Pino–Quercion*)

These are lowland and hill forests on yellow, quartz-allitic soils derived from slatey rocks. The canopy is 60–70% closed some plams and evergreen trees are intermingled with the pines. The cover of the rich shrub layer may be as much as 50%. The cover of herbs is close to 100% in the drier, convex geological formations. The Isla de Pinos representative of this vegetation type is the *Pinetum caribaeae-tropicalis* association (SAMEK 1969). Characteristic species are *Pinus tropicalis*, *Pinus caribaea*, *Acoelorrhaphe wrightii*, *Coccothrinax mira-*

guama, Curatella americana, Byrsonima crassifolia, Tetrazygia delicatula, Roigella correifolia, Croton craspedotrichus, Chamaesyce pinariona, Clitoria laurifolia, Evolvulus sericeus, Phyllanthus junceus, Zamia silicea, Panicum aciculare, Lyonia myrtilloides, Xylopia aromatica, Desmodium barbatum, Eriosema crinitum, Herpyza grandiflora, Trachypogon filifolius, and *Leptocoryphium lanatum.* In Pinar del Rio this community is replaced by mixed oak-pinewoods, *Querco sagraeanae-Pinetum,* that become oak gallery forests in the moist habitats of valleys. Typical species are *Pinus tropicalis, P. caribaea, Quercus sagraeana, Rhus copallina* ssp. *leucantha, Xylopia aromatica, Roigella correifolia, Tabebuia lepidophylla, Befarua cubensis, Vaccinium cubense* ssp. *ramonii, Tetrazygia delicatula, M. ibaguensis, Conostegia xalapensis, Byrsonia crassifolia, B. pinetorum, Davilla rugosa, Psidium salutare, Clidemia neglecta, Hypericum styphelioides* s. str., *Lygodium cubense, Pachyanthus poiretii, Chrysobalanus pellocarpus,* and *Odontosoria wrighitana.*

Pinus caribaea forests on ferritic soils (*Neomazaeo-Pinion caribaeae*)

This is the original paraclimax coniferous forests in the Cajalbana Hills. The canopy is fairly closed, a 70—80% cover is usual. Some degraded stands are of a loose 'woodland' character. On ridges and slopes the shrub layer is usually poor, the herb layer is dominated by grasses. On flat areas a vegetation type with shrubs and tall grasses develops. In the valleys the shrub layer is very dense and many fern species occur. All these are variants of the *Neomazaeo-Pinetum caribaeae* climax association. Its characteristic species are *Pinus caribaea, Coccothrinax yuraguana, Purdiaea cubensis, Eugenia rosariensis, Vaccinium cubense*

Fig. 14. Pinus caribaea forest on serpentine of the Cajalbana Hill (Pinar del Rio Province) with *Vaccinium cubense* ssp. *ramonii, Casearia silvestris* ssp. *myricoides, Eugenia rosariensis, Odontosoria wrightiana* (Photo: A. BORHIDI)

ssp. *ramonii*, *Sauvallella immarginata*, *Neomazaea phialanthoides*, *Acunaeanthus tinifolius*, *Psidium cymosum*, *Tabebuia leptopoda*, *Anemia cajalbanica*, *Mitracarpus glabrescens*, *Phania cajalbanica*, *Tetrazygia coriacea*, *Rondeletia longibracteata*, *Lescaillea equisetiformis*, *Andropogon*, *gracilis*, *Aristida refracta*, and *Rhynchospora tenuis*, etc. On steep rocky slopes the more open *Agavo cajalbanensi-Pinetum caribaeae* community is found. This is rich in agaves, palms and spiny shrubs. Of the many serpentine endemics *Agave cajalbanensis*, *Eugenia rigidifolia*, *Brya ebenus*, *Jacquinia brunnescens*, *Malpighia horrida*, *Buxus wrightii*, *Zanthoxylum dumosum* s. str. *Plinia dermatodes*, *Machaonia dumosa*, and *Rheedia fruticosa* are characteristic here.

Xerothermic Pinus cubensis forests (*Guettardo-Pinion cubensis*)

These are xerothermic coniferous forests on the ferritic soils of lowland and hilly serpentine areas and the more elevated, open rocky places of Sagua-Baracoa. These communities are very rich in endemics (67.74% of the presence scores). The ratio of regional and Cuban endemics is high: RE/CE = 4.2. The Greater Antillean species outnumber the Neotropical elements, their ratio being GA/Nt = 1.4. The microclimate in the relatively open stands is xerothermic. The highly developed shrub layer is microphyllous; many more phanerophytes occur than hemicryprophytes (P/H = 2.6). The percentage of spiny elements is over 10%. Four associations are distinguished. *Anemio-Pinetum cubensis* includes the climax pinewoods in the foothills and submontane belt of Nipe and Cristal. Characteristic species are *Pinus cubensis*, *Anemia coriacea*, *A. nipensis*, *Coccothrinax orientalis*, *Caesaria crassinervis*, *Ouratea striata*, *Clerodendron nipense*, *Lyonia macrophylla*, *L. nipensis*, *Vernonia urbaniana*, *Guettarda monocarpa*, *G. calyptrata*, *Bletia purpurea*, *B. floribunda*, *Plumeria clusioides*, *Pachyanthus reticulatus*, *Paepalanthus brittonii*, *Tabebuia shaferi*, *Vaccinium cubense* ssp. *cubense*, *Andropogon* spp., *Rhynchospora* spp., *Galactia rudolphioides*, *Rajania howardii*, and *Heptanthus cordifolius*. The foothills north of Moa and the hill-country of Baracoa are covered by very rich *Dracaeno-Pinetum cubensis* forests to about 400 m in altitude. The 72.4% of endemism is higher than all other cuban coniferous forest communities. Beneath the closed canopy there is a dense shrub layer of 40—50% cover, and a usually tall herb layer. Characteristic species are *Pinus cubensis*, *Dracaena cubensis*, *Schmidtottia shaferi*, *Psidium parvifolium*, *Casearia bissei*, *C. moaensis*, *Guettarda crassipes*, *Cyrilla cubensis*, *Ossaea pauciflora*, *Phyllanthus myrtilloides* ssp. *erythrinus*, *Jacquinia roigii*, *Myrtus ophiticola*, *Bumelia cubensis*, *Suberanthus stellatus*, *Rhynchospora lindeniana*, *Eugenia pinetorum*, *Guettarda ferruginea*, *Callicarpa oblanceolata*, and *Anemia coriacea* ssp. *moaensis*.

Two of the rocky coniferous forest communities may be classified into the group of the xerothermic pine forests. The *Agavo shaferi-Pinetum* association develops on the cliffs and even on the eroded mocarrero surfaces of the Nipe and Cristal mountains. Its canopy layer is loose (30—50%), the cover of shrubs is between 30 and 60%. Characteristic species are *Pinus cubensis*, *Coccothrinax orientalis*, *Agave shaferi*, *Ariadne shaferi*, *Aristida laevigata*, *Oplonia cubensis*, *Clusia nipensis*, *Cyrilla nipensis*, *Callicarpa nipensis*, *C. lancifolia*, *Eupatorium nipense*, *Euphorbia podocarpifolia*, *Gesneria nipensis*, *Ossaea acunae*, *Paspalum breve*, and *Platygyne triandra*, etc. On the eroded rocky ridges of Moa occur the *Euphorbio helenae-Pinetum cubensis* forests with dwarf palms, sometimes loose canopy, and a shrub layer of 70–80% cover. The characteristic species of this type are *Pinus cubensis*, *Coccothrinax moaensis*, *Euphorbia helenae*, *Scaevola wrightii*, *Croton monogynus*, *Coccoloba oligantha*, *Eupatorium lantanifolium*, *Guettarda ferruginea*, *Cochnatia recurva*, *Hypericum stypheloides* ssp. *moaensis*, *Linodendron aronifolium*, *Malpighia cnide*, *Neobracea valenzuelana*, *Rheedia ophiticola*, *Senecio trichotomus*, *Tabebuia pinetorum*, *Byrsonima minutifolia*, *Vaccinium alainii*, and *Vernonia wrightii*.

Mesophilous and montane Pinus cubensis forests (*Andropogono-Pinion cubensis*)

These are natural and semi-cultured stands of the paraclimax coniferous belt between 600–900 m on the ferritic latosols of the Sagua-Baracoa serpentine mountains. The proportion of endemics (52.4% of the total of presence scores) and the ratio of regional and Cuban endemics (RE/CE = 2.9) are lower than in the xerothermic *Pinus cubensis* forests. The Neotropical elements outnumber the Greater Antillean species (GA/Nt = 0.8). The natural stands are more closed than those abandoned by agriculturalists and, furthermore, the herb layer is tall and dense, the phanerophyte/hemicryptophyte ratio is low (P/H = 1.3), the spiny elements are absent in most cases (their frequency being lower than 5%). Two climax associations are distinguished. The *Rhynchosporo-Pinetum* association includes the montane pinewoods of the Nipe and Cristal mountains. It is characterized by eight *Rhynchospora* species and the abundance of *Baccharis scoparioides, Pteridium caudatum, Andropogon reinoldii,* and *A. nashianus.* Three types are recognized within this community. Type a, *panicetosum,* is found on flat and moderately sloping areas and contains *Clidemia capituliflora, Sauvagesia brownei Panicum aciculare. P. fusiforme, P. scoparium,* and *Paspalum alainii.* Type b, *rhynchosporetosum* occurs in hollows and valleys is a moister formation and has *Rhynchospora diodon, R. tenuis, R. shaferi, R. nipensis, R. lindeniana, Ternstroemia flavescens* and *Turnera diffusa,* etc. Type c, *euphorbietosum* is found on the shallow soils of mocarrero ridges, some of its species are *Euphorbia helenae, Croton borhidii, Lyonia macrophylla, Guettarda ferruginea,* and *G. calyptrata.* Type c is not recognized as a separate association, unlike the analogous situation in the Moa Mts.

In the high interior plateaux of Moa Mts (Cupeyal, upper Toa valley) is the much richer *Shafero-Pinetum* community. The 20–25 m high closed canopy layer is a mixture of pines and many evergreen trees. A second canopy layer composed of smaller trees, such as *Bactris cubensis* and *Alsophila aquilina,* is found underneath. Characteristic species are *Pinus cubensis, Spirotecoma apiculata, Miconia cerasiflora, Shafera platyphylla, Vaccinium alainii, Lyonia glandulosa, Eupatorium ayapanoides, E. grandiceps, Clethra cubensis, Ficus wrightii, Gomidesia lindeniana, Gundlachia cubana, Hyeronima nipensis, Ilex macfadyenii, Lisianthus glandulosus, Linociera domingensis, Chaetocarpus oblongatus, Miconia* spp., *Mecranium* spp., *Ossaea navasensis, O. ferruginea, Schmidtottia multiflora, Scolosanthus lucidus,* and *Vernonia calida.*

Mixed tree fern-pinewoods in the montane rainforest zone (*Pinetalia occidentalis-maestrensis*)

This vegetation type has been studied only in Hispaniola, stands are formed by *Pinus occidentalis* and develops between 1500–2500 m in the rainforest zone (Urban 1923, Ekman 1930, Ciferri 1936, Marie-Victorin 1943). Accompanying species are *Weinmannia pinnata, Garrya fadyenii* and many montane endemics. In Cuba such communities are represented by some isolated stands on the northern slopes of Sierra Maestra between 800–1300 m, on acidic yellow montane soils developed mainly on sandstone outcrops. In Pico Turquino there are stands reaching an elevation as much as 1800 m. In Grand Piedra, too, pinewoods occur in the montane rainforest zone. These had been considered *Pinus cubensis* stands, although the constituent trees may just as well be introgressive hybrids of *Pinus cubensis* and *Pinus occidentalis.* These morphologically rather diversified population were united under the name of *Pinus maestrensis* bisse. The variability range of its populations has been studied by A. López.

Savannas

The origin, spontaneous development and artificial change of the savannas of Cuba have been discussed in detail by BORHIDI and HERRERA (1977) BORHIDI (1987, 1988). The map shows both the original and the derived savannas and, in the latter case, indicates the original vegetation type. Based on physiognomy, two main groups of savannas can be distinguished: tall palm-tall grass savannas (*Sabalo-Roystonietea*) and small palm-dwarf grass savannas (*Coccothrinacio-Copernicietea*). The floristic composition has been started to study by BALÁTOVÁ and collab. (1983, 1985 a, b), earlier only lists containing 'savanna trees and grasses' of each province have been published (SEIFRIZ 1943). These lists, however, cannot characterize adequately the flora of physiognomic units. Furthermore, SEIFRIZ's floristical data are occasionally erroneous and species never found together are often given in the same list. As these lists should be treated with caution, only the structure and ecology of savannas will be described here.

SAVANNA AND GRASSLAND VEGETATION

Roystonea-Ceiba agricultural savannas (*Ceibo-Roystonion*)

Cultivated lands on the rich ferrallitic soils on the lowlands of central Cuba, especially Matanzas and Habana clays, where seasonal rainforest was the original vegetation. Characteristic trees are large specimens of *Ceiba pentandra* and *Spondias mombin*, loaded with epiphytes, and *Roystonea regia*, *Chrysophyllum oliviforme*, *Genipa americana*. The herb layer is rich in species, e.g. *Andropogon virginicus*, *A. pertusus*, *Paspalum notatum*, *P. distichum*, *P. fimbriatum*, *Panicum caespitosum*, *P. reptans*, *P. boliviense*, *P. adspersum*, *P. dichotomiflorum*, *Cyperus iria*, *C. haspan*, *C. ligularis*, *C. flavus*, *C. surinamensis*, *Cuphea melanium*, *C. parsonsia*, *Borreria ocimoides*, *Setaria geniculata*, *S. tenax*, *Sporobolus indicus*, *Reynaudia filiformis*, *Dichromena ciliata*, *Gomphrena decumbens*, *Rhynchelytrum roseum*, and *Macroptilium lathyroides*, etc.

Roystonea agricultural savannas (*Samaneo-Roystonion*)

These are savannas of the semi-deciduous forest zone on moderately rich siallitic lowland soils, in a seasonal climate with 4–8 dry months. Characteristic seed-bearers are *Roystonea*, *Samanea*, *Peltophorum adnatum*, *Pithecellobium cubense*, *Cordia gerascanthus*, *C. dentata*, *Psidium guajava*, *Anacardium edule*, and *Bursera simaruba*. The components of the herb layer are mainly those of the previous type, although most *Cyperus* species are replaced by *Sclerias*. Tall savanna grasses not native to Cuba (e.g., *Panicum maximum*, *Hyparrhenia rufa*) are commonly planted and became established.

Copernicia agricultural savannas (*Andropogono-Copernicietalia*)

These are secondary savannas of the semi-deciduous dry forest and dry evergreen forest zone. Small fragments developed as a result of edaphic conditions, may be natural. These stands were extended by logging and burning the neighbouring forests. The secondary savannas are usually found on poor sandy or mocarrero soils, the latter may be secondarily developed after deforestation in wet gallery forests. Characteristic species are *Copernicia*

baileyana, C. gigas, C. vespertilionum, C. sueroana, C. molineti, C. rigida, C. burretiana, C. textilis, C. hospita, in some places also *C. roigii, C. clarkii*, and *C. humicola*. (The dwarf *Copernicias* of serpentine shrublands occur in the short grass savannas. Here and there spiny trees with loose canopy, such as *Belairia mucronata* and *Acacia* species, may occur intermingled with the seed-bearers. The herb layer is composed of a great variety of plants, mainly *Andropogon* and *Rhynchospora* species (*Andropogon virginicus, A. bicornis, A. brevifolius, A. reedii, Rhynchospora diodon, R. tenuis, R. cyperoides*) and *Panicum chrysopsidifolium, Fimbristylis annua, Bulbostylis setacea, Buchnera elongata, Anisantherina hispidula, Pterocaulon alopecuroideum, Cassia rotundifolia, C. insularis, Schultesia guianensis, Stylosanthes hamata, Zornia diphylla, Sebastiania corniculata, Borreria ocimoides*, and *B. thymocephala*, etc.

Dwarf palm agricultural savannas on serpentine
(*Parvicopernicio-Coccothrinacion*)

These communities are considered by most authors as natural savannas which rapidly spread following the degradation of the original dry shrublands of serpentine zones with seasonal arid climate. Small, 1–4 m high palms are common as standard trees, for example the vicarious serpentinophilous ecotypes of *Copernicia macroglossa, Coccothrinax miraguama* and *Copernicia glabrescens* in Matanzas, *C. hospita* ssp. *clarensis* in Las Villas, *C. yarey* in Camagüey and Oriente, *C. cowellii* and *Coccothrinax pseudorigida* in Camagüey, *Coccothrinax garciana* and *C. nipensis* in Oriente. The relatively high *Gastrococos crispa* savannas of wetter or richer serpentine soils are also included here. The herb layer is dominated by dwarf grasses, namely *Andropogon* and *Aristida* species *Andropogon hirtiflorus, A. multinervosus, Aristida neglecta, A. refracta, A. vilfifolia*, which also occur in the shrublands. Other species to be mentioned are *Imperata brasiliensis, Diodia rigida, D. teres, Solanum aculeatum, Byrsonima crassifolia, Sachsia polycephala, Ayenia euphrasifolia, Croton nummulariifolius, Leptocoryphium lanatum, Polygala saginoides, Stylosanthes hamata, Angelonia pilosella, Thymopsis thymoides Evolvulus sericeus*, and *Zamia kickxii*, etc.

Fig. 15. Dwarf palm agricultural savanna on the serpentine of Camagüey, with *Copernicia cowellii, C. hospita, Coccothrinax camagüeyana, C. pseudorigida* and var. *acaulis*. (Photo: A. BORHIDI)

Pine savannas (*Pino-Aristidion neglectae*)

These secondary communities replace degraded pinewoods on yellow allite-ferrite soils on quartz and slate substrates, or on red ferrallitic soils. Scattered individuals of pine are still present, the herb layer is the same as in the previous type.

Natural and seminatural edaphic Sabal savannas (*Macrocopernicio-Sabalion*)

These savannas usually develop on mocarrero soils containing an impermeable layer close to the surface and having a strong seasonal fluctuation of moisture content. Most stands are found in the provinces of Pinar del Rio, Matanzas and Las Villas. The floristic composition of these formations is not sufficiently known. Characteristic elements are the dominant *Sabal parviflora*, and in the herb layer *Rhynchospora*, *Scleria* and *Setaria* species. Notable plants are the endemic *Cheilophyllum* species.

Secondary Sabal savannas

The widespread *Sabal* palm swampy meadows and moist pastures have been derived from the wet gallery forests of coastal zones and from the fenwood stages of the vegetational succession in boggy hollows. The floristic composition is determined by the former quality of habitats, the methods of land use and the intensity of land exploitation. Tropical black or meadow soils, and occasionally peaty soils are typical. The secondary *Sabal* savannas are not distinguished from the gallery forests and bogs in the map.

Acoelorraphe wrightii savannas

These are either degraded forms of *Acoelorrhapho-Pinion* pinewoods on sands, secondary communities derived from deforested fenwoods, or, in some cases, stages of the natural reforestation of bogs (meadows with palms and tall sedges). Being relatively small, these are included in the categories of sandy pinewoods and bogs in the map.

Deciduous and treeless savannas

These stands are usually the results of the complete transformation of the wet alluvial forest belt found parallel to the coasts. The origin of these savannas was revealed by the study of soils and geomorphology. VORONOV (1970) describes many such areas from Camagüey and Oriente, but they are of heterogeneous origin and their separation is doubtful. These stands are shown as areas of potential alluvial forest on the map. Treeless grasslands have been studied on different soils and bedrocks by BALÁTOVÁ-TULÁČKOVÁ and coll. On seasonally flooded alluvial and mocarrero soil she described two communities: *Gossypiantho brittonii–Aristidetum refractae* and *Byrsonimo-Andropogonetum teneris* (1983). On the serpentine of Camarioca (Matanzas province) an extremely degraded grassland community: *Cassio lineatae–Aristidetum neglectae* (1985) occurs. They described also some communities from the white sand area of Isle of Pines and the limestone of the Sierra del Rosario (1982, 1985).

FRESHWATER VEGETATION FORMATIONS

Alluvial forests

These forests occur in the wide valleys of lowland rivers, especially along the Cauto, on the coastal alluvial cones of smaller rivers, and in flatlands bordered by small rivers and the coast. The soils are rich tropical black soils or tropical meadow soils (term 'meadow' refers merely to soil type and not vegetation) they are under water in the wet season and do not dry out even in the dry season. The forests, with a single canopy layer and emergent *Roystonea* palms, are 20–25 m high. In places covered by water for longer time the height is 10–15 m and emergent *Sabal* palms occur. Most trees are partially deciduous, e.g. *Bucida subinermis*, *Tabebuia angustata*, and *Erythroxylon confusum*. The diverse epiphyte layer is composed mainly of drought-resistant heliophytic *Tillandsias*. Contrary to the epiphytes, the lianes are macrophyllous hydrophytic species (e.g. *Philodendron krebsii*, *Vanilla articulata*). Characteristic species are *Roystonea regia*, *Sabal parviflora*, *S. japa*, *Acoelorrhaphe wrightii*, *Bucida buceras*, *Hibiscus elatus*, *Calophyllum antillanum* ssp. *rivularis*, *Tabebuia angustata*, *Swietenia mahagoni*, *Guettarda combsii*, *Ficus subcabrida*, *Myrsine cubana*, *Tabernaemontana amblyocarpa*, *Crescentia cujete*, and *Conocarpus erecta*. In the herb layer *Cladium jamaicense*, *Acrostichum danaifolium*, *Nephrolepis biserrata*, *Enhydra sessilis*, *Bacopa* spp., *Haenianthus* spp., *Paspalum vaginatum*, *Dichromena colorata*, *Cyperus acicularis*, *C. articulatus*, *Fimbristylis annua*, *F. spathacea*, and *Aster* spp. occur. Following the removal of gallery forest trees *Roystonea* groves and savannas, second-grown *Sabal* groves and savannas, various mixed deciduous savannas (with *Bucida*, *Swietenia*, etc.) and treeless savannas may develop, depending on the type of habitat and intensity of land exploitation.

Riverain forests and derived types

The gallery forests along rivers and creeks are rich in lianes, palms and tall grasses and have only a single canopy layer. Characteristic elements are *Roystonea regia*, *Calyptronoma dulcis*, *Lonchocarpus domingensis*, *Lysiloma bahamensis*, *Dalbergia ecastophyllum*, *Bucida buceras*, *Ginoria americana;* of the lianes *Arthrostylidium cubense* and *A. capillifolium*, and of the tall grasses *Gynerium sagittatum*, the latter forming dense stands like reeds. Most natural stands have been replaced by secondary vegetation, such as *Roystonea* lines, *Bambusa vulgaris* bushes, and *Arundo donax* stands. The *Calyptronoma* galleries along mountain streams have been almost completely removed. They are succeeded by dense stands of the introduced *Syzygium jambos* and by second-growth marginal stands of *Pennisetum purpureum* and *Cyperus alternifolius*.

Swamp vegetation complex

Just like in the temperate zone, the vegetation of bogs and swamps is a mosaic of several noda with dissimilar structure and composition which is determined by the quantity of accumulated litter. Therefore, all uliginal vegetation types are included in a single category in the map. The succession starts with floating plants followed by submersed and rooted weeds of ponds. Then, *Eleocharis interstincta*, *E. cellulosa*, *Scirpus validus*, *S. olneyi* and later *Typha domingensis* associations follow. Skipping the *Scirpus* stage, *Typha domingensis* may directly form small floating stands ('marsh islets'). Along watercourses *Typha* may be replaced by *Cyperus giganteus*. The next stage of the successional sere is occupied by *Cladium jamaicense* which grows to a height of 1.5–2 m. In sites always covered by water the *Crino-Cladietum*

association is found, otherwise *Pontederio-Cladietum* develops. This is the earliest stage in which fenwood elements may be encountered, e.g. *Acoelorrhaphe wrightii, Chrysobalanus icaco* and *Annona glabra*, and then tall *Sabal parviflora* palms (*Chrysobalano-Annonetum* Ciferri 1936). Subsequently, high fenwoods (*Tabebuio-Bucidetum*) with *Bucida palustris, Tabebuia angustata, Hibiscus elatus, Fraxinus caroliniana* ssp. *cubensis*, and *Salix longipes* develop. In the meantime *Sabal* is gradually replaced by *Roystonea*. Logging and grazing result in boggy meadows or wet *Sabal* (or *Roystonea*) cultured savannas. On limestone substrate, bogs are succeeded by low karstic fenwoods (*Osmundo-Annonetum*) with many ferns and epiphytes. On sandy beaches of lagoons fern-palm shrubwoods (*Blechno-Acoelorrhaphetum* HADAČ 1971) represent the subsequent stage. The latter association occurs in the zone of sandy pinewoods.

Freshwater weed communities

Extensive stands, large enough to show in the map, are associated with the major lakes (Ariguanabo, Laguna del Tesoro). In deep water a floating layer of duck-weed (*Lemno-Azollehem carolinianae, Salvietum auriculatae*) and floating mats of water-hyacinth and water-lettuce (*Eichhornietum crassipedis* and *E. azureae, Pistietum stratiotidis* Ciferri 1936) develop. Submerged floating bladderworts are also present forming communities of the *Aldrovando-Utricularion* alliance. In the ponds and slow streams of the Zapata peninsula the submerged and rooted *Vallisneria* forms a community (*Vallisnerietum neotropicalis*). Extensive aquatic communities of other localities are composed of *Cabomba piauhiensis* and *Myriophyllum sparsiflorum*. In Laguna del Tesoro *Vallisneria neotropicalis, Potamogeton nodosus* and *P. illinoensis* are found in large stands. Rooted mats of water-lily, lotus and fringed water-lily are also significant. Major constituents of freshwater weed communities are *Brasenia schreberi, Nymphaea ampla, N. odorata, Nuphar advena, Nymphoides grayanum, Nelumbo lutea, Polygonum portoricensis* and *Limnocharis flava*. In the shallow coastal zone of sandy lagoons a very special floating community formed by the moss-like *Mayaca wrightii* is found.

COASTAL VEGETATION

Mangroves (*Rhizophoro-Avicennietea*)

The Caribbean mangrove vegetation, composed only of four tree species, has been studied in several localities (CIFERRI 1936, ASPREY and ROBBINS 1953, STEHLÉ 1945, HOLDRIDGE 1940, DANSEREAU 1966, LOVELESS 1960, and DAVIS 1940, 1942). Besides floristic surveys, some reports on the growth and regeneration (WADSWORTH 1959), ecology (DAVIS 1940) and nutrient cycling (GOLLEY, ODUM and WILSON 1962) of mangrove communities are known. In Cuba, as elsewhere, mangrove vegetation occurs along shallow muddy beaches protected by coral reefs. Here mangroves may form zones 2–3 km wide. In estuaries with a shallow gradient (Hatiguanico, Cauto) mangroves penetrate deeply into the island following saltwater from high tides. In the intertidal zone *Rhizophora mangle* forms a belt between the low tide and normal levels, whereas *Avicennia nitida* is dominant between the normal and high tide levels. In some *Avicennia* stands *Languncularia racemosa* individuals are intermingled. The *Rhizophoretum* community is usually free from accompanying species. In contrast, the *Avicennia* mangrove has many special elements, such as *Acrostichum aureum, A. danaifolium, Rhabdadenia biflora, Cynanchum salinarum, Lycium carolinianum*, and *Batis maritima*. In the uppermost section of the intertidal zone an extremely salt-resistant species, *Conocarpus erecta*, forms pure stands or it may be mixed with *Laguncularia* and *Avicennia* mixed stands. Salt deposit zone up to 1 km wide is commonly found in the landward edge

of the *Conocarpus* belt. This area is under water only during the equinoctial periods. The vegetation of salt deposits is composed of *Batis maritima*, and occasionally also of *Suaeda linearis* and *Salicornia perennis*. Due to its small size, this saltwort vegetation is included in the mangroves on the vegetation map.

The vegetation of sandy beaches (*Ipomoeo-Tournefortietea*)

The plant communities of sandy beaches are found particularly well developed between Habana and Varadero, and also in the Guanahacabibes peninsula, in the southern part of Isla de Pinos, and in several short sections of the southern coast of Cuba. Two noted pioneer plants of the strand line are *Ipomeoa pes-caprae* and *Canavalia maritima*. They are common in the open strand communities such as *Sesuvio-Ipomoeetum*, *Ipomoeo-Philoxeretum*, and *Philoxero-Unioletum virgatae*. The community type actually occurring in a site is determined by the hardness of ground, angle of slope and water supply. The next successional stage is the horse-bush scrub (*Borrichio-Mallotonietalia*) with various combinations of *Borrichia arborescens*, *Mallotonia* (*Tournefortia*) *gnaphaloiaes*, *Spartina juncea*, *Turnera diffusa*, *Ernodea maritima*, *Suriana maritima*, *Baccharis halimifolia*, and *Sporolobus virginicus*. The primary dunes are covered by sea-grape (*Coccoloba uvifera*) scrubs. Towards the interior of the island this successional sere is terminated by dry coastal evergreen scrubs ('manigua costera').

The coastal rock pavement vegetation (*Sesuvio-Rhachicallidetea*)

The communities of coastal rocky slopes are especially widespread along the southern coast of eastern and central Cuba and at Habana and Matanzas. In contrast to the sandy vegetation, which is primarily of pan-tropical character, the vegetation of coastal rock pavements is mainly of Antillean and Caribbean elements. Most constituents of the open pioneer community (*Trianthemo-Sesuvietalia*) are succulent creepers (*Lithophila muscoides*, *Trianthema portulacastrum*, *Sesuvium portulacastrum*, *S. maritimum*). The next successional stage is the coastal rocky scrub (*Borrichic-Rhachicallidetalia*) containing *Rhachicallis americana*, *Borrichia arborescens*, *Erithalis fruticosa*, *Strumpfia maritima*, *Conocarpus erecta*, *Flaveria linearis*, *Heliotropium humifusum*, *Pectis* spp., *Opuntia dillenii*, and *Agave legrelliana*. Many scrub associations may be distinguished. On cliffs exposed to salt-spray and winds *Rhachicallis* and *Conocarpus* form a community, which is similar to some alpine creeper communities in appearance. Further up these stands may reach a height of 1.5 m. Then, low sea-grape scrub follow on shallow sand. Elsewhere, e.g. in northwestern and southeastern Oriente, this sea-grape stage is skipped and thorn scrubs occur. These thorn scrubs are rich in Mimosaceae species.

ACKNOWLEDGEMENTS

The autkor is thankful to Dr. J. Podani for the English version, and to J. Tanner, Botany School, Cambridge, for the critical reading of the text.

REFERENCES

Acuña, J. G. 1964: Flora de las ciénagas de Cuba. — *Poeyana*, Ser. A. No. 3. 10 pp.
Alain, H. Liogier 1950: Notas sobre la vegetacion de la Loma de Cajalbana, Pinar del Rio. — *Rev. Soc. Bot. Cubana* **7.** (1–2–3): 8–18.
Ascanio, O., Perez, J. M., Hernandez, A. 1968: Mapa genético de los suelos de Cuba 1:1000 000 — Inst. de Suelos Acad. Scien. de Cuba.
Ashton, P. S. 1964: A quantitative phytosociological technique applied to tropical mixed rain forest. — *Malay. For.* **27:** 307–317.
Asprey, G. F., Robbins, R. G. 1953: The Vegetation of Jamaica. — *Ecol. Monogr.* **23:** 359–412.

Aubréville, A. M. 1965: Princeps d'une systématique des formations végétales tropicales. — *Adansonia* **5:** 153—196.
Balátová-Tuláčková, E., R. P. Capote 1982: A new savanna-like community of the Sierra del Rosario Mountains, Cuba. — *Folia Geobot. Phytotax.* **17:** 137—148.
Balátová-Tuláčková, E., R. P. Capote 1985a: Contribution to the knowledge of some savanna and forb-rich communities on the Isla de la Juventud (Cuba). — *Folia Geobot. Phytotax.* **20:** 17—39.
Balátová-Tuláčková, E., R. P. Capote, 1985b: The *Cassio lineatae Aristidetum neglectae*, a new association of the serpentine in Cuba. — *Folia Geobot. Phytotax.* **20:** 177—183.
Balátovó-Tuláčková, E., M. Surli 1983: Contribution to the phytosociological characteristics, of the Yaguaramas Savannas (Cienfuegos Province, Cuba). *Folia Geobot. Phytotax.* **18:** 1—12.
Beard, J. S. 1942: Montane vegetation in the Antilles. *Caribbean For.* **3:** 61—74.
Beard, J. S. 1944: Climax vegetation in tropical America. — *Ecol.* **25:** 127—158.
Beard, J. S. 1946/b: The Mora forests of Trinidad, British West Indies. — *Ecology* **33:** 173—192.
Beard, J. S. 1949: The natural vegetation of the Windward and Leeward Islands. *Oxford Forest. Mem.* **21.**
Beard, J. S. 1953: The Savanna Vegetation of Northern Tropical America. — *Ecol. Monogr.* **23:** 149—215.
Beard, J. S. 1955: The classification of tropical American vegetation types. — *Ecol.* **36:** 89—100.
Beard, J. S. 1967: Some Vegetation Types of Tropical Australia in relation to those of Africa and America. — *J. Ecol.* **55:** 271—290.
Bennett, H. H.—Allison, R. V. 1928: *The Soils of Cuba.* — Washington 410 pp.
Borhidi, A. 1973: *Fundamentals of Geobotany of Cuba.* — Tesis for D. Sc. habil. Budapest, 292 pp. + 78 Figs and Tabs. + 5 maps.
Borhidi, A. 1974: *Kubában térképeztünk.* (Mapping in Cuba) — Budapest, Gondolat pp. 245 + 116 Tab.
Borhidi, A. 1985: Phytogeographic survey of Cuba I. The phytogeographic characteristics and evolution of the flora of Cuba. — *Acta Bot. Hung.* **31:** 3—34.
Borhidi, A. 1988: Vegetation dynamics of the savannization process on Cuba. — *Vegetatio* **77:** 177—183.
Borhidi, A. 1989: Efectos de la roca serpentina en la adaptación y evolución de la flora y vegetatión tropical en Cuba. — *Acta Bot. Hung.* **34.**
Borhidi, A., R. Herrera, 1977: Génesis, caracteristicas y clasificación de los ecosistemas de sabana en Cuba. — *Ciencias Biol. Acad. Cien. Cuba* **1:** 115—130.
Borhidi, A., Muñiz, O. 1980: Die Vegetationskarte von Kuba. — *Acta Bot. Acad. Sci. Hung.* **26:** 25—53.
Borhidi, A., Muñiz, O., Del-Risco, E. 1979: Clasificación fitocenológica de la vegetación de Cuba. — *Acta Bot. Acad. Sci. Hung.* **25:** 263—301.
Borhidi, A., Muñiz, O., Del-Risco, E. 1983: Plant communities of Cuba. I. Fresh and salt water, swamp and coastal vegetation. — *Acta Bot. Acad. Sci. Hung.* **29:** 337—376.
Ciferri, R. 1936: Studio geobotanico dell'Isola Hispaniola (Antille). — *Atti. d. Ist. Bot. Univ. Pravia* **8:** 3—336.
Dansereau, P. 1951: Description and recording of vegetation upon a structural basis. — *Ecol.* **32:** 172—229.
Dansereau, P. 1957: *Biogeography. An Ecological Perspective.* — Ronald Press Co. New York,
Dansereau, P. 1958: An universal system for recording vegetation. — *Contr. Inst. Bot. Univ. Montreal* **72:** 58 pp.
Dansereau, P. 1966: Studies on the vegetation of Puerto Rico, I. — *Univ. of Puerto Rico Spec.* Publ. No. 1 1—45.
Dansereau, P., Buell, F. P. 1966: Studies on the vegetation of Puerto Rico II. — *Ibidem* 46—287.
Davis, J. H. 1940: The ecology and geologic role of mangrove in Florida. — *Carnegie Inst. Washingt. Publ.* **517:** 303—412.
Davis, J. H. 1942: The ecology of the vegetation and topography of the sand keys of Florida. — *Ibidem* **524:** 115—195.
Del-Risco, E., Borhidi, A. 1975: Estructura del manto vegetal. In: Informe sobre el estado de los conocimientos relativos a los ecosistemas forestales tropicales de Cuba; bosques perennifolios, semicaducifolios. Informe al UNESCO, 23—43.
Eiten, G. 1972: The Cerrado Vegetation of Brasil. — *Bot. Review* **38:** 201—341.
Ellenberg, H., Mueller-Dombois, D. 1966: Tentative physiognomic ecological classification of plant formations of the Earth. — *Ber. Geobot. Inst. Rübel* **37:** 21—56.
Gill, T. 1931: *Tropical Forests of the Caribbean.* Washington 318 pp.

Golley, F., Odum, H. T., Wilson, R. F. 1962: The Structure and Metabolism of a Puerto Rican Red Mangrove Forest in May. *Ecol.* 43: 10–19.
Grubb, P. J. Lloyd, J. R., Pennington, T. D., Whitmore, T. C. 1963: A comparison of montane and lowland rain forest in Ecuador I. The forest structure, physiognomy and floristics. — *J. Ecol:* **51.** 567–601.
Hadač, E., Hadačová, V. 1971: The Association Blechno serrulati-Acoeloraphetum wrightii in the Remates de Guane, W-Cuba, and its Ecology. — *Folia Geobot. Phytotax*, **6:** 369–388.
Holdridge, L. R. 1940: Some notes on the mangrove swamps of Puerto Rico. — *Caribb. Forester* **1:**(4) 19–29.
Holdridge, L. R. 1967: *Life Zone Ecology*. — San José, 206 pp.
Holdridge, L. R., Gronke, W. C., Hatheway, W. H., Liang, T. and Tosi, J. A. Jr. 1971: *Forest Environments in Tropical Life Zones.* A pilot study.
Howard, A. R. 1968: The ecology of an elfin forest in Puerto Rico. I. Introduction and composition studies. — *J. Arn. Arb.* **49:** 381–418.
Howard, A. R. 1969: The ecology of an elfin forest in Puerto Rico. VIII. Studies of stem growth and form and of leaf structure. — *J. Arn. Arb.* **50:** 225–262. + 5 tab.
Howard, A. R. 1974: *The Vegetation of the Antilles.* In: Vegetation and vegetation history of Northern Latin America. Ed. A. Graham, Elsevier, New York. 1–38.
Hueck, K. 1966: *Die Wälder Südamerikas.* — Fischer, Jena 422 pp.
Hueck, K., Seibert, P. 1972: *Vegetationskarte von Südamerika* — Stuttgart, Fischer· 69 pp.
Knapp, R. 1965: *Die Vegetation von Nord- und Mittelamerika.* — Fischer Stuttgart—Jena 373 pp.
León, H. Sauget 1946: *Flora de Cuba.* Vol. 1. Contrib. Ocas.Mus. Hist. Nat. Col. La Salle, No. 8. 441 pp. La Habana.
Lötschert, W. 1955: La vegetación de El Salvador. *Com. Inst. Trop. Inv. Ci.* **4:** 65–79.
Lötschert, W. 1958: Die Übereinstimmung von geologischer Unterlage und Vegetation in der Sierra de los Organos (West-Cuba). *Ber. Deutsch. Bot. Ges.* **71:** 55–70.
Lötschert, W. 1959: Vegetation und Standortsklima in El Salvador. *Bot. Studien* **10:** 1–88.
Loveless, A. R. 1960: The vegetation of Antigua, W. Indies. *J. Ecol.* **48:** 495–527.
Loveless, A. R., Asprey, G. F. 1957: The dry evergreen formations of Jamaica. I. J. *Ecol.* **45:** 799–822.
Loveless, C. M. 1959: A study of the vegetation in the Florida Everglades. *Ecology*, **40:** 1–9.
Marie-Victorin, F. 1943: Les haut pinèdes d'Haiti. *Contr. Inst. Bot. Univ. Montreal* **48:** 47–60.
Samek, V. 1969: La vegetación de la Isla de Pinos. — *Acad. Cien. de Cuba, Ser. Isla de Pinos*, No. **28:** 28 pp. + 2 tab.
Seifriz, W. 1943: The plant life of Cuba. — *Ecol. Monogr.* **13:** 375–426.
Stehlé, H. 1945: Forest Types of the Caribbean Islands. Part I. *Caribbean For.* **6.** Suppl. 273–422.
Stoffers, A. L. 1956: *The Vegetation of the Netherlands Antilles.* Utrecht, 142 pp.
Urban, I. 1923: Zur Pflanzengeographie von Hispaniola. — *Symb. Ant.* **9:** 1–54.
Urban, I. 1924–1928: Plantae cubenses novae val rariores a clo. E. L. Ekman lectae. — Ibidem **9:** I. fasc. 1. 55–176. — II. fasc. 2. 177–272 (1924). — III. fasc. 3. 398–432 (1925). — IV. fasc. 4. 435–543 (1928).
Voronov, A. G. 1970: Mapa de vegetation. — *Atlas Nacional de Cuba.* pp. 56–59.
Wadsworth, F. H. 1959: Growth and regenaration of White Mangrove in Puerto Rico. — *Caribbean For.* **20:** 59–72.

Acta Botanica Hungarica 33 (3—4), pp. 187—197 (1987)

THE MACROPHYTE VEGETATION OF A SMALL BRANCH-SYSTEM OF THE DANUBE AT DUNAREMETE (SZIGETKÖZ, RIVER km 1826)

(DANUBIALIA HUNGARICA CX)

B. RÁTH

DANUBE RESEARCH STATION, HUNGARIAN ACADEMY OF SCIENCES, GÖD

(Received: December 1, 1986)

This paper presents an overview on the macrophyte vegetation of a small branch-system of the Danube river at Szigetköz. Plant community types and the life form spectra of species are discussed. The spatial localization of stands and its relation to the accumulation of silt are demonstrated by a map; the zonation of vegetation is shown by profile diagrams. Data are presented on the phytomass and the accumulation of biotic elements (N, P) of species. The results suggest that the area has favorable habitat characteristics and nutritional status.

Introduction

The study of the floodplain of Danube at Szigetköz has received considerable attention recently. The construction of the Gabčikovo-Nagymaros Dam-system causes the disappearance of the natural habitats and the change of fauna and flora in this area. In the middle part of Szigetköz, the expected decrease of water level will cause exceedingly great changes in the conditions of life of the macrophyte vegetation of the river. Therefore, it is extremely important to explore and register the present status of vegetation before construction work begins.

With the above facts in mind, I performed hydrobotanic studies at Dunaremete (River km 1826) in 1984–1985, in a small branch system which will be influenced by the abandoned riverbed after the dam system is finished. The stands of the macrophyte vegetation were coenologically analyzed, information on the biomass was collected, and the nitrogen and phosphorous content of plants was measured.

On the macrophytes of the branch system at Dunaremete there is no report in the literature. POLGÁR's (1941) floristic studies were restricted to the environs of Győr, KÁRPÁTI V. (1963) was concerned only with the coenology and ecology of larger branch systems (Cikola-, Doborgaz-islands, etc.) and the Moson Danube Branch. My results therefore may contribute to our knowledge on a less intensively studied part of the natural history of Szigetköz.

Methods and study area

The branch system examined is located on the floodplain between the river and the embankment, north of Dunaremete (Fig. 1). The watercourses are lined with gallery forests and reed stands, the latter are sometimes quite extensive. The total length of three branches is about 5200 m, their width ranges from a few metres to 200 m. The largest branch (Szilos) with open water has a permanent connection with the Danube river through a narrow "gate" left on the embankment. At a distance of 1700 m, two smaller branches are formed. The smaller, canal-like branch (Csatorna) turns toward the Danube; the broader branch (Fanos) turns toward Kisbodak village. Water movement is proportionally slower with the distance from the river, and the remote section of Fanos is in fact a dead branch.

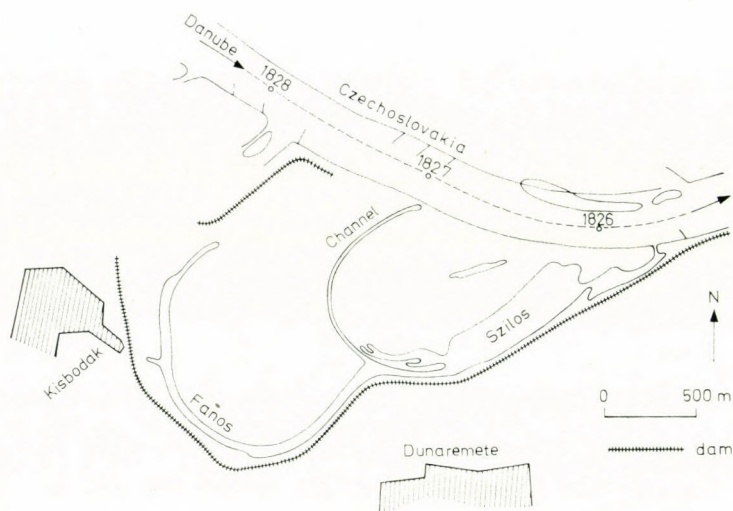



Fig. 1. Map of the side-arm system at Dunaremete

The shore of the branch system is deeply inclined toward the embankment and mostly flat, sometimes marshy toward the river. The substrate is variable: sandy mud in Szilos, which is the closest to the Danube, and muddy in the other two branches.

The light conditions are favourable. Only Szilos is exposed to strong winds, since it is less protected by gallery forests.

The water is the deepest at the junction of the branch system, 216 cm at medium water level. Water depth decreases to 160–120 cm as distance from the junction increases; in the muddy ends of branches the depth is only 50–60 cm.

Water supply comes directly from the Danube at high water level (over 450 cm on the water-gauge at Dunaremete). When water level is lower, water is infiltrated through the gravel bed from the river.

The fluctuation of water level at medium water, as it happened during field work, was negligible (30–50 cm).

According to our preliminary chemical analysis of the water, the branch system is rich in oxygene, its pH and electric conductivity are similar to those of the main branch (Table 1).

Table 1

Some physical and chemical characteristics of the river Danube and its side-arm system at Dunaremete (at River km 1826)

Date	Sampling sites	Water level cm	Water temperature °C	O_2 dissolved mg/l	O_2 saturation %	pH	Conductivity μS
3. 7. 1984	main arm	398	15	9.8	97	7.88	268
3. 7. 1984	Szilos		18.5	9.3	100	7.87	277
14. 8. 1984	main arm	456	19	8.3	90	7.55	281
14. 8. 1984	Szilos		18	8.8	94	7.60	276
7. 5. 1985	main arm	408	10.2	12.6	112	8.74	362
7. 5. 1985	Szilos		14	17.6	172	9.16	352
26. 6. 1985	main arm	465	14.2	10.0	98	8.21	287
26. 6. 1985	Szilos		18	12.6	134	8.66	312

The coenological analysis was performed according to BRAUN-BLANQUET's relevé technique using the AD scale.

The phytomass was measured in the flowering period of plants, using the so-called water-monolith technique, from a water column of 0.25 m^2 basal area and actual depth, in three replicates. When selecting the number of replicate samples and the area, the homogeneity of stands and the relatively high (60–70%) cover values were considered. The aboveground part of plants was weighed after desiccation at 105 °C. Plant production is given for 1 m^2 (GULYÁS 1983) and in the maximum maturity period it stands for the annual production.

The total N and P contents were measured by the KJELDAHL method in the aboveground parts (leaves, stems). The percentages are given for dry weight (FELFÖLDY 1980).

Results and discussion

Macrophyte vegetation

The favorable hydrological and ecological conditions (slow movement of water, low depth, muddy substrate, rich nutrition supply) of the branch system at Dunaremete allowed the development of an aquatic vegetation so characteristic of still waters.

One-fourth of the water surface (the total surface is 28 ha) is covered by a homogeneous reed stand. The largest continuous reed stand occurs in Szilos, together with some large islets of reed which divide the water surface into many smaller branches. On the last 400 m section of Szilos, the homogeneous reed community is replaced by reeds intermingled with marsh vegetation or by bulrush. The reeds of Fanos are standing in water and are restricted to a narrow strip along the shore.

In bays lined with reeds and in the open water of muddy branch sections aquatic weeds occur. The plant cover as estimated in the field was 10% in Szilos, 40% in Fanos and 5% in Csatorna. The life-form spectrum of weed species (SHENNIKOV 1953) is influenced by the closeness of the Danube as the most important habitat condition.

Most common are the rooting weeds that are less sensitive to waves and water movement (the submersed *Potamogeton* species; and *Nuphar lutea* out of the floating weeds). Characteristic are the amphibious plants which tolerate strong fluctuations of the water level (*Polygonum amphibium* f. *natans*, *Rorippa amphibia*). Weeds less protected against strong currents (the submerged *Ceratophyllum demersum*, the floating *Lemna* species) are less abundant.

The coenological relevés indicate that the most significant association of macrophytes is the *Nymphaeetum albo-luteae* Nowinski 1928. Its extensive stands occur in both Szilos and Fanos at a depth of 90–150 cm. Its submersed layer, contrary to similar communities known from the dead branches of the Danube river (KÁRPÁTI V. 1963, RÁTH 1978–1979, OT'AHELOVA 1980) is lacking. Therefore, the floristic composition is relatively poor. In its three subassociations, almost only the naming species occur (Table 2).

Of the less significant communities, the *Myriophyllo-Potametum potametosum lucentis* Soó 1957 occurs in the shallow water near the bank of Szilos, and *Myriophyllo-Potametum potametosum perfoliati* Soó 1934 in the deeper open water of it. In the latter community type, the protected *Nymphoides peltata* is worth mentioning (Table 3). *Polygonetum natantis* Soó 1927, which is transitional toward the marsh vegetation (*Rorippa amphibia*), is found in the very shallow, muddy part of Szilos as well (Table 4). In the Csatorna, which is the slowest stream, smaller patches of *Ceratophylletum demersi* (Soó 1927, HILD 1956, DEN HARTOG et SEGAL 1964) developed (Table 5).

As to the spatial arrangement of communities, the alluvial processes described in dead branches and mortlakes of the Tisza and Dráva (CHOLNOKY 1907, KOVÁCS and KÁRPÁTI 1973), that is, the upper sections have older and the lower ones younger deposits, are well-seen (Fig. 2). Accordingly, in the section closest to the Danube the pioneer stands of *Myriophyllo-*

Table 2

Nymphaeetum albo-luteae Nowinski 1928, life form-groups of the species (after Shennikov)

Subassociation	Nupharetosum					Typicum				Nymphaeetosum					
Samples	1	2	3	4	5	6	7	8	9	10	11	12	13	A—D	K
Cover %	50	50	60	40	30	70	50	80	60	70	90	30	50		
Depth cm	125	90	90	120	120	110	100	100	150	110	90	120	100		
Submerged floating															
Ceratophyllum demersum	.	.	.	1	+	.	.	.	.	.	.	.	.	+—1	I
Submerged rooted in sediment															
Potamogeton perfoliatus	.	.	.	.	(+)	.	.	.	.	.	.	.	.	+	A
Potamogeton crispus	.	.	.	.	+	.	.	.	.	.	.	.	.	+	A
Floating on the surface															
Lemna minor	.	+	.	.	.	.	.	.	.	.	.	.	.	+	A
Floating and rooted in sediment															
Nymphaea alba	.	.	.	.	.	4	3	1(3)	2	4	5	3	3	1—5	IV
Nuphar lutea	3	3	4	3	3	+	+(1)	4	3	.	.	.	.	+—4	IV
Emerging above water															
Schoenoplectus lacustris	.	1(3)	.	.	.	.	.	1(3)	.	.	.	.	.	1—3	I
Phragmites australis	.	.	.	.	.	.	.	.	.	.	.	.	1(3)	1—3	A

Plot size: 5×5 m

Locality: 1, 6, 7, 8, 10. : Szilos
2, 3, 11. : Szilos
9, 13. : Szilos
4, 5, 12. : Fanos

Date: 13. 6. 1984
3. 7. 1984
26. 6. 1985
14. 8. 1984

Table 3

Myriophyllo-Potametum Soó 1934, life form-groups of the species (after Shennikov)

Subassociation	Potametosum lucentis				Potametosum perfoliati							
Samples	1	2	3	4	5	6	7	8	9	10	A—D	K
Cover %	50	50	30	60	30	50	60	70	80	50		
Depth cm	70	50	60	70	100	80	160	180	120	80		
Submerged floating												
Cladophora sp.	.	.	.	.	.	.	+	+	4	3	+—4	II
Ceratophyllum demersum	.	.	.	.	.	.	.	.	1	+	+—1	I
Submerged rooted in sediment												
Potamogeton perfoliatus	.	+	1	1	3	3	4	4	4	2	+—4	V
Potamogeton lucens	3	3	3	4	.	.	.	.	.	.	3—4	II
Floating on the surface												
Lemna minor	.	+	.	.	.	.	.	.	+	+	+	II
Floating and rooted in sediment												
Nymphoides peltata	.	.	.	.	.	.	.	.	.	1	1	A
Polygonum amphibium f. *natans*	.	.	.	+	.	.	.	.	.	1	+—1	I
Emerging above water												
Rorippa amphibia	+	.	(4)	(4)	.	.	.	.	(+)	+	+—4	II
Rumex hydrolapathum	.	.	.	+	.	.	.	.	+	.	+	I
Salix alba	.	.	.	.	.	.	.	.	(+)	(+)	+	I
Carex gracilis	.	.	.	.	.	.	.	.	.	+	+	A
Glyceria maxima	.	.	.	.	.	.	.	.	.	+	+	A

Plot size: 5×5 m   Locality: Szilos   Date: 2– 6. : 13. 6. 1984
2– 6. : 3. 7. 1984
7–10. : 26. 6. 1985

Potametum potametosum perfoliati occur. In the remote, more alluvial sections with open water *Nymphaeetum albo-luteae nupharetosum*, and where even more alluvial deposits occur (e.g. along the shore or in bays among reeds) *Nymphaeetum albo-luteae nymphaeetosum* and *Polygonetum natantis* are characteristic. The advanced alluvial stage and the increasing nutrient concentration are indicated by *Ceratophylletum demersi.*

Table 4

Polygonetum natantis Soó 1927, life form-groups of the species (after Shennikov)

Samples Cover % Depth cm	1 75 60	2 50 70	3 75 70	4 70 60	5 80 100
Submerged rooted in sediment					
Potamogeton perfoliatus	+	+	+	+	1
Potamogeton lucens	.	.	+	.	.
Floating and rooted in sediment					
Polygonum amphibium f. *natans*	4	3	4	4	4–5
Emerging above water					
Rorippa amphibia	3	1	(4)	(3)	.
Rumex hydrolapathum	+	.	.	.	.
Salix triandra	(+)	.	(3)	.	.
Iris pseudacorus	.	(1)	.	.	.

Plot size: 5×5 m
Locality: Szilos
Date: 1–2. : 13. 6. 1984
3–4. : 3. 7. 1984
5. : 26. 6. 1985

Table 5

Ceratophylletum demersi (Soó 1927, Hild 1956, Den Hartog et Segal 1964), life form-groups of the species (after Shennikov)

Samples Cover % Depth cm	1 80 140	2 30 165	3 60 160	4 50 160	5 70 180
Submerged floating					
Ceratophyllum demersum	4	3	4	3	4
Floating on the surface					
Lemna minor	+	.	+	.	.
Spirodela polyrrhiza	1	.	1	.	.
Floating and rooted in sediment					
Nuphar lutea	.	1	.	+	.

Plot size: 3×2 m
Locality: Csatorna
Date: 26. 6. 1985

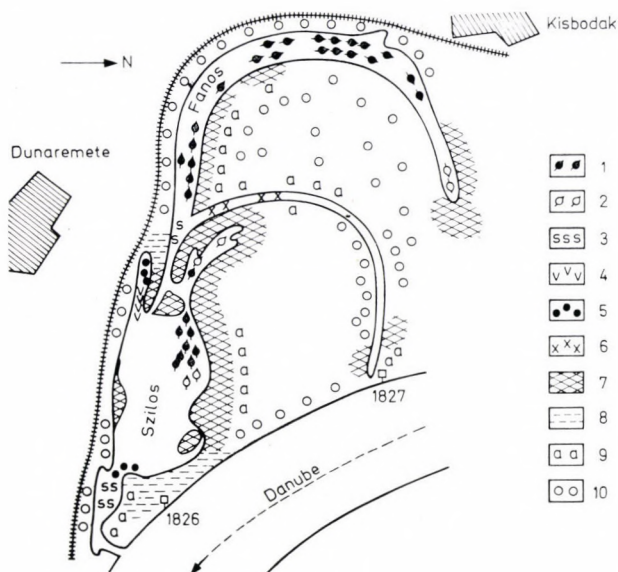



Fig. 2. Distribution of plant communities in the side-arm system at Dunaremete
1. ***Nymphaeetum albo-luteae nupharetosum***, 2. ***nymphaeetosum;*** 3. ***Myriophyllo-Potametum potametosum perfoliati***, 4. ***potametosum lucentis;*** 5. ***Polygonetum natantis***, 6. ***Ceratophylletum demersi***, 7. ***Scirpo-Phragmitetum***, 8. ***Rorippa amphibia*** stand, 9. ***Salicetum triandrae***, 10. ***Salicetum albae-fragilis***.

It is typical of the branch system that no macrophytes are established in a large part of the open water in Szilos. This is due to the strong NW winds and especially to the more intensive water movement in the branch, rather than to the depth factor (depth is 160 cm on the average) and to the absence of appropriate substrate. The zonation of communities as affected by depth is shown by the profile diagrams of Fig. 3. In the deepest part *Nymphaeetum albo-luteae*, and then as depth decreases reeds (*Scirpo-Phragmitetum*) occur. The aquatic weed and reed zones are broad (in Szilos) or narrow (in Fanos), depending on the slope angle of the bank. The reeds are followed by willow thicket (*Salicetum triandrae*) and then, as elevation increases, willow-poplar gallery forest (*Salicetum albae-fragilis*). This series of communities is considered by SIMON (1978) as a potential successional series in areas of the low Danube floodplain with fluctuating water level.

Phytomass

The production of dominant species (*Nuphar lutea*, *Nymphaea alba*, *Potamogeton perfoliatus*) of three communities (*Nymphaeetum albo-luteae nupharetosum*, *Nymphaeetum albo-luteae nymphaeetosum*, *Myriophyllo-Potametum potametosum perfoliati*) were measured (Table 6).

Nuphar lutea yields the highest phytomass. Greater values were obtained in 1984 (526.6 g.m^{-2}). The reason of the lower 1985 values is probably that the habitat conditions (high water, cool spring) were less favorable in that year.

The phytomass of *Nymphaea alba* is lower than that of the *Nuphar lutea* stands (328.6 g.m^{-2}), but its production was measured only in one year.

The cover of *Potamogeton perfoliatus* is only a few % in the study area. Its phytomass was quite considerable (353.5 g.m^{-2}) in 1985, however, when water level was high.

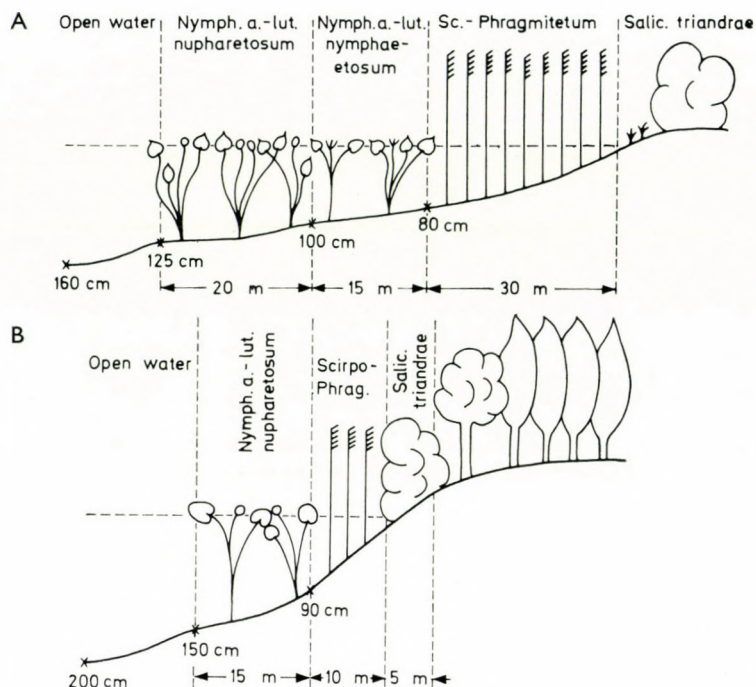



Fig. 3. A Zonation of the macrophytic communities at the sampling site Szilos (13. 7. 1984)
B Zonation of the macrophytic communities at the sampling sites Fanos (26. 6. 1985)

According to the literature, the natural eutrophic waters are characterized by high *Nymphaea* and *Nuphar* production. In the Kisbalaton, for example, the fresh production was 4740 g.m^{-2} (its 10% is the dry weight, cf. KÁRPÁTI V. 1977). OT'AHELOVA and HUSAK (1985) report on high phytomass values measured in *Nuphar lutea* stands in the Eastern Slovakian Plain: 1417 g.m^{-2}. In advanced alluvial stages, the production of Nymphaea alba also increases: 500 g.mw^{2} in the Danube delta (KLOKOW 1977) and 519 g.m^{-2} in the Öreg Duna dead branch at Baja. In eutrophic water the phytomass of submersed plants is also significant. In normally developed stands it is about 300–350 g.m^{-2}, and may be as high as 600 g.m^{-2} in extremely developed ones (KRAUSCH 1976). Several autors (JORGA and WEISE 1977, MAYER 1982) assert that the submersed phytomass over 250 g.m^{-2} my have negative consequences in the eco-system and deteriorates water quality. For comparison, the phytomass of Potamogeton perfoliatus in oligotrophic lakes (Ladoga, Onyega, Ilmeny) is 30–143 g.m^{-2} (RASPOPOV 1985), and in Lake Balaton in 1969 it was 80 g.m^{-2} in dry weight (KÁRPÁTI I. and VARGA 1970).

Nitrogen and phosphorous accumulation

The side branches of Szigetköz are rich in nutrients (TEVANNÉ 1982). The macrophytes, as N and P accumulators, are suitable to the bioindication of nutrient richness. However, we must also consider the fact that the N and P concentration of plants is correlated not only with the N and P content of the water but is influenced by many other factors and differs with species, physiology, developmental stage of plants and organs, etc. (DYKYJOVA and PETROVA 1983).

Table 6

Phytomass production, N *und* P *content of several macrophytic species in the side-arm system at Dunaremete* (*River* km 1826)

Phytomass production

Macrophytic species	Date of sampling	Water depth cm	Average production g ·m^{-2}
Nymphaea alba	3. 7. 1984	90–110	328.6
Nuphar lutea	3. 7. 1984	90–125	526.6
	26. 6. 1985	150	367.3
Potamogeton perfoliatus	26. 6. 1985	160–200	353.5

N and P content

Date of sampling:	3. 7. 1984	N %	P %
Potamogeton crispus		1.92	0.42
Ceratophyllum demersum		1.83	0.39
Potamogeton lucens		1.83	0.36
Potamogeton perfoliatus		1.65	0.38
Polygonum amphibium f. *natans*	leaf	1.66	0.35
	stem	0.79	0.30
Nuphar lutea	leaf	1.50	0.33
	stem	1.00	0.27
Nymphaea alba	leaf	1.33	0.31
	stem	0.85	0.31

The N concentration of aquatic weeds in the study area varies between 1.33 and 1.92% (Table 6). The relatively high N accumulation of *Potamogeton crispus* was also observed in other parts of the Danube (Ráth 1984). The different N concentration of the two parts of the leaves of floating plants (i.e. the blade and the petiole) shows that the N compounds of the water and deposits are mostly accumulated by the assimilatory organs.

If compared with other results published by Dykyjova and Petrova (1983), the N content of aquatic weeds is medium. Similar N concentrations were measured by Kovács and Tóth (1979) in the aquatic weeds of the open water of Lake Balaton (1.5–2%); the percentages for plants living in the shoreline were slightly higher (2–3.5%).

The phosphorous accumulation of macrophytes depends on the P concentration of water, as confirmed by the laboratory experiments of Wagner (1966). Regarding the P content of the water in the Dunaremete branch-system, there are only approximate data available (80 mg.m^{-3} dissolved P). Nevertheless, the slightly higher scores of plants (0.31–0.42%) suggest that sufficient P supply is available for the plants. *Potamogeton crispus* accumulates the most P, like N, therefore this species may be regarded as a good indicator of nutrient load.

Species with floating leaves contain less P, and there is no difference between leaf blade and petiole (Table 6). According to published data (Raspopov 1985), the average P concentration of aquatic plants is 0.2–0.3%. In storage lakes 0.4% (Korelyakova 1970, Yakubovski 1979) and in strongly eutrophic water 0.7–0.8% (Smirnova 1984) were obtained.

Summary

My studies showed that in the Dunaremete side-branch system of the Danube (Szigetköz, at 1826 km), a diverse vegetation corresponding to different successional stages on alluvial deposits has developed. Well reflecting the hydrological conditions (slow water movement, variable depth), the rooted species (*Nuphar lutea*, *Potamogeton* species) predominate.

The most significant community is the *Nymphaeetum albo-luteae*. Of its two constant species, especially *Nuphar lutea* forms extensive stands. In sections with less favorable conditions (water level fluctuation, waves, etc.), *Myriophyllo-Potametum* is found, whereas in areas with mud accumulation *Ceratophylletum demersi* and *Polygonetum natantis* occur in small stands.

The phytomass production corresponds to that of natural eutrophic waters with medium alluvial deposits: 327—527 $g.m^{-2}$. *Nuphar lutea* yields the highest production, it is 447 $g.m^{-2}$ on the average of two years.

The N content of plants is about the usual (1.33—1.92%), whereas the P content is slightly higher (0.31—0.42%).

Potamogeton crispus, which accumulates the highest amounts of P and N, indicates that nutrient supply of the study area is good; its sporadic occurrence refers to the less advanced eutrophication of the waters.

REFERENCES

Cholnoky, J. 1907: A Tiszameder helyzetváltozásai. *Földr. Közl.* **35:** 381–405, 425–445.

Dykyjova, D., Košánova, A., Husák, S., Sladečkova, A. 1985: Macrophytes and water pollution of the Zlata Stoka (Golden Canal) Třeboň Biosphere Reserve, Czechoslovakia. *Arch. Hydrobiol.* **105:** 31–58.

Dykyjova, D., Petrova, I. A. 1983: Chimicheskiy sostav makrofitov i faktorü, opredelyayushchiye koncentraciu mineralnykh veshchestv v vysshick vodnykh rastenyiyakh. In: Gidrobiologicheskiye processi v vodoyomach (ed.: Raspopov, I. M., Hejny, S.). Leningrád, Nauka. 107–212.

Felföldy, L. 1980: A biológiai vízminősítés. In: Vízügyi Hidrobiológia 9 (ed.: Felföldy, L.). VIZDOK Bp. pp. 263.

Gulyás, P. 1983: KGST Biológiai módszerek. In: Vízügyi Hidrobiológia 12 (ed.: Felföldy, L.). VIZDOK Bp. pp. 244.

Jorga, W., Weise, G. 1977: Biomasseentwicklung submerser Makrophyten in langsam fliessenden Gewässern in Beziehung zum Sauerstoffhaushalt. *Int. Revue ges. Hydrobiol.* **62:** 209–234.

Kárpáti, I., Varga, Gy. 1970: A Keszthelyi öböl hínárvegetációja kutatásának eredményei (Forschungsergebnisse der Laichkrautvegetation in der Balatonbucht von Keszthely). *A Keszthelyi Agrártudományi Főiskola Közleményei.* **12:** 3–58.

Kárpáti, V. 1963: Die zönologischen und ökologischen Verhältnisse der Wasservegetation des Donau-Überschwemmungsraumes in Ungarn. *Acta Bot. Acad. Sci. Hung.* **9:** 323–385.

Kárpáti, V. 1977: A Kisbalaton vízi vegetációja és a jellemző fajok tápanyagakkumulációs képessége. *MTA Veszprémi Akadémiai Bizottságának Értesítője* III. 131–140.

Klokow, V. M. 1977: Vodnaya rastitelnosty i floristicheskiye osobennosti Kiliyskoy Delty Dunaya. Avtoref. diss. kand. biol. nauk. Moszkva, pp. 20.

Korelyakova, I. L. 1970: Chimicheskiy sostav vysshey vodnoy rastitelnosti Kievskovo vodochranilishcha. *Gibrobiol. Zhurnal* **6:** 20–27.

Kovács, M., Kárpáti, I. 1973: A Mura- és a Dráva-ártér vegetációja. *Földr. Ért.* **22:** 21–31.

Kovács, M., Tóth, L. 1979: A balatoni hínárok biogén-elem felhalmozásáról. *VITUKI Közl.* **14:** 49–74.

Krausch, H. D. 1976: Die Makrophyten der mittleren Saale und ihre Biomasse. *Limnologica* **10:** 57–72.
Mayer, H. G. 1982: Biomassen submerser Wasserpflanzen — ein landwirtschaftlicher Sekundärrohstoff. *Acta Hidrochim. Hydrobiol.* **10:** 55–59.
Oťahelova, H. 1980: Makrofytné spoločenstvá otvorených vod Podunajskej roviny (Trieda Lemnetea, Potamogetonetea). *Biologické Práce XXVI.* pp. 175.
Oťahelova, H., Husák, S. 1985: Vodna a močiarka vegetacia. In: Vegetačné pomery juznej časti Vychodoslovenskej niziny. *Acta Bot. Slovaca* "A", **8:** 44–115.
Polgár, S. 1941: Győrmegye flórája. Flora comitatus Jaurinensis. *Bot. Közl.* **38:** 201–352.
Raspopov, I. M. 1985: Vüsshaja vodnaja rastitelnost bolshih ozer Severo-Zapada USSR· Leningrád, Nauka. pp. 197.
Ráth, B. 1978–1979: Untersuchung der Laichkrautvegetation eines toten Armes in der Umgebung von Baja. (Danubialia Hungarica LXXXV) *Ann. Univ. Sci. Bp.* **20/21:** 137–153.
Ráth, B. 1978–1979: Laichkraut-Phytomassenuntersuchungen in toten Arm "Alte-Donau" bei Bátmonostor (Südungarn). (Danubialia Hungarica LXXXVI). *Ann. Univ. Sci. Bp.* **20/21:** 155–162.
Ráth, B. 1984: Änderung des N- und P- Gehaltes der submersen Wasserpflanzen in der Vegetationsperiode. *Kurzreferatum,* 24. *Arbeitstagung der IAD, Szentendre.* 175–178.
Shennikov, A. P. 1953: A növények ökológiája. Bp. pp. 456.
Simon, T. 1978: A Gabcsikovo-Nagymarosi Vízlépcsőrendszer létesítésével összefüggő biológiai egyensúly vizsgálata I. ELTE Növényrendszertani és Ökológiai Tanszék. Bp. Kézirat. pp. 206.
Smirnowa, N. N. 1984: Die Akkumulation von den biogenen Elementen und Schwermetallen durch die höheren Wasserpflanzen im Kiliadelta der Donau. Kurzreferatum, 24. *Arbeitstagung der IAD, Szentendre.* 179–182.
Tevanné Bartalis, É. 1982: A Duna szigetközi holtágainak kémiai-biológiai vizsgálata a vegetációs időszakban (1978–80). In: *Vízminőségi Évkönyv* (*VITUKI*) 1980. *Bp.* 173–196.
Wagner, G. 1966: Phosphatspeicherung und N/P Quotient bei Laichkräutern in abwasserbelasteten und unbelasteten Ufergebieten des Bodensees. *Int. Revue Ges. Hydrobiol.* **51:** 229–235.
Yakubovski, K. B. 1979: Chimicheskiy sostav vysshikh vodnykh rastenyiy na raznykh etapakh ih vegetatsii, deformatsii i razlozheniya. In: Melkovodya Kremenchugskovo vodochranilishcha. Kiev „Naukova Dumka". 75–82.

Acta Botanica Hungarica 33 (3—4), pp. 199—210 (1987)

STATISTICAL RELATIONSHIPS BETWEEN THE ORDINATION OF COENOLOGICAL RELEVÉS AND CHARACTERISTIC INDICATOR VALUES

I. Bagi

DEPARTMENT OF PLANT SCIENCES, A. JÓZSEF UNIVERSITY, SZEGED

(Received: September 10, 1986)

Starting from the assumption that ordinations are capable of revealing the same features that are expressed by indicator values of species in a given community, the validity of published indicator values may be checked using statistical methods, and the scores may be modified if necessary. A functional relationship between the indicator values (X) and the result of ordination (A) is sought such that $X = g(x)$, where x is the environmental variable indicated, and $A = f(x)$ which expresses the partial dependence of ordination results on the environmental variable. In the linear case, $\frac{df(x)}{dg(x)} = C$, and the correlation between f(x) and g(x) and the coefficient of variation of C can easily be calculated.

The usefulness of the method is demonstrated by RA and CFA ordinations of *Elatini-Eleocharition ovatae* communities of riverbeds and the indicator values of their species as suggested by Ellenberg, Soó and Zólyomi. The application of TWINSPAN (two-ways indicator species analysis) is suggested to modify indicator values according to the ordination results. The changes are coenologically meaningful as the features of an indicator value system, within which modifications are proposed, were all considered when making the suggestions.

Introduction

The characteristic indicator values summarize information on the environmental requirements of species in large areas (geobotanical or geographical regions). However, in studies of particular communities sometimes great differences may occur between actual values (valid to the particular community type within a region, e.g. for the species of the *Bidention*, *Elatini-Eleocharition ovatae* and *Chenopodion rubri* in the floodplains of Carpaticum) and published scores, especially in case of coenologically indifferent species.

The problem with characteristic indicator values will be clarified if we examine the way in which they were constructed.

The underlying assumption is that vegetation indicates the environment (concordance principle, Juhász-Nagy 1970, 1984). The indicator value for a species is determined by the frequency of that species in communities with different ecological requirements. This step is much influenced by the experience of the author regarding the distribution of the species. If the process of data collection and processing is interpreted as a special case of sampling, then the problems with indicator values will be associated with basic statistical terms of sampling: communities in which the species is present (statistical population), the experience of the author on the distribution of the species (representativity), the frequency of species in different communities (weighting), and the role of subjectivity in determining indicator values (bias).

Table 1

Coenological data table

Relevé number total percentage cover	1 20	2 85	3 20	4 75	5 60	6 95	7 30	8 90
1. *Dichostylis micheliana*	36	2	43	6	11	+	38	+
2. *Cyperus fuscus*	20	2	17	10	11	+	20	4
3. *Echinochloa crus-galli*	2	3	2	2	1	14	3	3
4. *Bidens tripartita*		1		1	1	6	+	2
5. *Polygonum lapathifolium*	2	+	1	+	15	26	3	+
6. *Rumex stenophyllus*	4	21	2	7	1	4	2	17
7. *Lythrum salicaria*	7	17	7	4	8	8	4	3
8. *Agrostis stolonifera*		+		4		+		1
9. *Polygonum hydropiper*						8		
10. *Chenopodium album*		1		+	+	4		
11. *Xanthium italicum*		2	3	+	8	6		
12. *Plantago major* ssp. *pleiosperma*	8	9	9	3	4	6	10	9
13. *Potentilla supina*		5		2		1		4
14. *Tanacetum vulgare*		4		1	1	5	1	3
15. *Chenopodium rubrum*	5	2	2	17	12	4	3	4
16. *Amaranthus lividus*	+	4	+	1	2	+	2	7
17. *Lythrum virgatum*		+	1	+	3	2		+
18. *Rorippa sylvestris*	4	9	4	22	8	3	5	34
19. *Veronica anagallis-aquatica*	2	3	1	+	3	2	+	
20. *Chenopodium ficifolium*					1	1		
21. *Salix triandra* (juv.)		1		1	+	+		
22. *Gnaphalium uliginosum*	8	5	5	17	8	+	6	9
23. *Oenanthe aquatica*	+	4			+	+		
24. *Chenopodium polyspermum*			+		2		2	
25. *Veronica beccabunga*	2	4	+	+				
26. *Chenopodium chenopodioides*			3	+				
27. *Juncus effusus*		1		+				
28. *Portulaca oleracea*							1	+
29. *Atriplex hastata*		+		+				+
30. *Amaranthus retroflexus*		+		+				+
31. *Ranunculus sceleratus*				1				
32. *Typhoides arundinacea*								
33. *Juncus bufonius*				1				
34. *Cirsium arvense*								
35. *Malva neglecta*								
36. *Juncus compressus*								
37. *Heleochloa alopecuroides*							+	
38. *Myosoton aquaticum*								

Species with cover values lower than 1%: *Alisma lanceolatum* 6; *Artemisia vulgaris* 10; *Chlorocyperus glomeratus* 2, 4, 7, 8, 13, 14, 16; *Hibiscus trionum* 10; *Limosella aquatica* 2, 4, 13, 14; *Lycopus europaeus* 6, 10, 14, 15, 16; *Lysimachia vulgaris* 13, 15; *Matricaria maritima* ssp. *inodora* 2, 4, 6; *Mentha arvensis* 15; *Potentilla reptans* 10; *Rorippa islandica* 14; *Sonchus asper* 6, 10, 13; *Taraxaxum officinale* 2, 14; *Trifolium repens* 2; *Urtica dioica* 8, 10, 14.

These problems may be raised only if the author's judgement on the actual value of environmental variable is correct. If the number of influential factors may be reduced — for example, because all relevés originate from the same community type and/or the environmental factor does not change significantly with seasons (cf. Bohus 1984), — then measurements of the variable may serve as a basis for determining the indicator values. The estimation

and indicator values

9	10	11	12	13	14	15	16	K	indicator value			I_j
70	85	85	80	35	75	40	70		E	Z	S	
9	+	2		13	4	55	25	V	9	10	8	+2.397
17	+	58	+	23	4		10	V	9	10	8	+1.276
13	13	6	20	+	4	+	3	V	5	9	7	−0.999
+	1	+	15		6	+	+	V	8	9	7	−0.646
3	4	+	3	9	+		+	V	7	9	7	−0.596
	4		2	+	16	2	5	V	6	7	6	−0.551
7	10	+	8	4	2	3	7	V	8	9	8	−0.436
+	6	+	10	5	4	+		IV	6	8	7	−0.410
+	6			+	2		+	II	8	9	7	−0.386
4	8		2		6			III	4	5	0	−0.380
1	1	3	10	9	+	+	+	V	6	7	6	−0.377
9	10	17	4	18	6	15	12	V	7	7	5	+0.307
	2				8		1	III	8	7	10	−0.238
+	4		+	2	2		3	IV	5	7	7	−0.228
5	7	+	2		6		13	V	6	7	6	−0.222
3	+	2	3		+		1	V	4	6	5	−0.103
4	3			1	+			IV	7	8	8	−0.090
9	10	6	1			19	5	V	8	8	6	−0.065
								II	9	9	9	−0.036
1	1			5				II	6	6	6	−0.028
4	4	3	+			5	+	IV	8	10	8	+0.021
3	+	1	5	9	8		15	V	7	9	7	−0.016
					4			III	10	11	10	
3		+						II	6	7	7	
					2			II	10	9	9	
1	1			1				II	6	7	6	
					6			II	7	9	8	
3	2						+	II	4	2	4	
				+	4			II	6	5	6	
	2		2					II	4	5	5	
					+	1		II	9	9	10	
		2	5					I	8	10	7	
					6			I	7	9	7	
		+	5					I	×	4	0	
	+		3					I	5	6	5	
				1			+	I	7	9	8	
1								I	6	6	6	
	1							I	8	8	6	

of moisture conditions, however, is usually subjective, and the measurements may even be misleading. In conclusion, the published indicator values apply to all community types of the area (large geographic region) examined by the author, but their determination involves several subjective elements. This is the reason that different indicator value systems do not necessarily agree regarding the response of a given species to environment.

The ecological application of indicator values (i.e. when environmental variables are estimated using the vegetation) involves the same sampling problems, especially representativity, that we are faced with before the construction of indicator value systems.

It is a common problem in coenological practice to know how precise is the description of the interspecific relationships in terms of a given environmental factor in a given indicator value system. The validity of characteristic indicator values for a given community type

Table 2

The g(x) *functions and ordination*

Relevé number	1	2	3	4	5	6	7
g(x) ELLENBERG	8.20	7.17	8.19	7.14	7.31	6.45	8.01
g(x) ZÓLYOMI	9.18	8.02	9.07	8.06	8.46	8.24	9.04
g(x) SOÓ	7.42	6.76	7.84	6.76	6.93	6.59	7.25
RA axis 1. — f(x)	03	61	05	44	48	94	07
RA axis 2.	17	06	25	14	42	42	29
CFA axis 1.	0.812	.190	.868	.551	.523	—.255	.927
CFA axis 2.	0.343	—.415	.330	—.453	—.205	.258	.252
CFA — f(x)	9.60	—2.18	9.60	1.53	2.90	—9.60	9.18

may be checked by ordination, if we assume that ordinations reflect in some way the examined features of the system. If we find a functional relationship between an ordination descriptor (A) and an environmental variable (x) such that $A = f(x)$, and if the indicator values (X) are linear and adequate descriptors of the environmental variable, i.e. $X = g(x)$, then for linear functions the ratio of their differential quotients will be constant:

$$\frac{df(x)}{dg(x)} = C \qquad (1.1)$$

Depending on the ordination results, $A = f(x)$ is linear or transformed to linear. Taking $f(x)$ as a characteristic function for the given community type, we can draw conclusions on $g(x)$ by examining the departure of the ratio from a constant value.

Statistical methods

Product moment correlation coefficient was used to measure linear dependence of $f(x)$ and $g(x)$ which exists if

$$df(x) = C\, dg(x) \text{ (according to 1.1)}$$

and then

$$f(x) = C\, g(x) + C' \qquad (2.1)$$

In addition, if successive coenological relevés from the same community show a variability large enough to neglect errors in cover estimates, then the constant C of eq. 1.1 will be worth examining for the following reasons:

$$f(x_1) = C\, g(x_1) + C'$$
$$f(x_2) = C\, g(x_2) + C'$$
$$f(x_1) - f(x_2) = C\, [g(x_1) - g(x_2)]$$
$$\Delta f(x) = C\, \Delta g(x)$$

$$\frac{\Delta f(x)}{\Delta g(x)} = C \qquad (2.2)$$

The higher the correlation coefficient (r) between $f(x)$ and $g(x)$ and the smaller the coefficient of variation (V) of C calculated for the relevé pairs, the "better" the characteristic indicator values.

loadings for relevés

8	9	10	11	12	13	14	15	16
6.96	7.06	6.44	8.10	6.03	7.52	6.78	8.37	7.50
7.74	8.48	7.69	9.13	7.99	8.55	7.98	7.07	8.59
6.22	6.62	6.12	7.18	6.20	7.01	6.76	7.15	7.16
55	44	82	15	100	34	76	0	26
06	53	34	100	40	70	10	0	17
.265	.558	—.086	.499	—.234	.637	.174	.672	.916
—.462	—.345	.554	—.193	.291	—.271	—.225	.308	—.012
—1.31	2.40	—11.6	3.30	—9.90	3.32	—3.54	8.92	6.80

A condition of the application of statistical methods is the correct estimation of the role of environmental variable, therefore an "x" environmental variable is to be measured in order to determine $f(x)$ (WARCHOLINSKA 1978, GIBSON et al. 1985). In exceptional cases no measurements are necessary if "x" monotonously changes within the period of study.

Material and multivariate methods

The indicator values used in this paper have been obtained from ELLENBERG (1974), ZÓLYOMI et al. (1967) and SOÓ (1964—1980). Indicator values not published in the literature may be determined according to personal experience, and considering the features of the given indicator value system (ZÓLYOMI and PRÉCSÉNYI 1964). These values are underlined in Table 1.

The coenological data table presents the relative cover of species in percentages. + indicates that the species was represented by a single individual in the relevé.

The mean characteristic indicator value of "water requirement" (W_i) for each relevé is calculated as an arithmetic mean weighted by the cover values of species. In the sequel, these values will correspond to g(x).

In the ordination a reduced data matrix (species 1–22 in Table 1) was involved; this matrix contains species with constancy values from III to V, and also some species with constancy value of II whose mean cover value is higher than 0.5%. The calculations were performed by BASIC programs (BAGI and KÖRMÖCZI 1986) written for centroid factor analysis (CFA) (LAWLEY and MAXWELL 1963, JAHN and VAHLE 1968) according to PRÉCSÉNYI's (1981) flow chart and for reciprocal averaging (RA) (HILL 1973).

The indicative ability of each species within the communities examined was revised using the first step of a divise clustering strategy (two-ways indicator species analysis, TWINSPAN) (HILL, BUNCE and SHAW 1975). The

$$I_j = \left| \frac{m_1}{M_1} - \frac{m_2}{M_2} \right|$$

binary formula was replaced by

$$I_j = \frac{m^+ \sum_{i=1}^{m+} m_j^+ f_i^+}{M^+ f^+} - \frac{m^- \sum_{i=1}^{m-} m_j^- f_i^-}{M^- f^-} \qquad (2.3)$$

for cover values, which is calculated as a weighted difference from the centroid of points in the ordination. The denotations are as follows:

I_j is the indicative ability of species j,

m_j^+ is the cover of species j in the positive side,

m^+ is the number of relevés in the positive side of the ordination,
f_i^+ is the difference of the coordinate of relevé i in the positive side on axis 1 from the centroid of all points. The centroid is

$$f = \frac{\sum_{i=1}^{m}{}' f_i}{m}$$

where f_i is tne loading of relevé i on axis 1 and m is the total number of relevés,
M^+ is the total cover of relevés on the positive side, and
f^+ is the mean distance of relevés on the positive side from the centroid.
The meaning of the symbols for the negative side is self-explanatory. HILL et al. (1975) provide a full description of terminology used above.

Application of the method to riverbed communities

The drying shores of the river are characterized by a monotonously changing moisture content in the soil, especially in the *Elatini-Eleocharition* ovatae zone of the muddy shore (TÍMÁR 1950). The gradual desiccation of soil is of decisive importance in the development of communities. The rapid change of vegetation, which characterizes the *Elatini-Eleocharition* ovatae zone, facilitates the collection of relevés as if they were come from different successional stages in the same area. Thus, in the ordination the direction of change is easily shown and A may be approximately determined.

In the study area, first species of *Elatini-Eleocharition ovatae* Pietsch 65 occur, they compose the *Cypero-Juncetum bufonii* Soó et Csűrös (27) 44 and *Dichostylidi-Gnaphalietum uliginosi* (Horvatić 31) Soó et Timár 47 communities, and their intermediate types (PIETSCH 1973). Finally, mixed communities of *Bidention tripartitae* (Koch 26) Libbert 32 character replace the desorganized *Elatini-Eleocharition* associations (UJVÁROSI 1940).

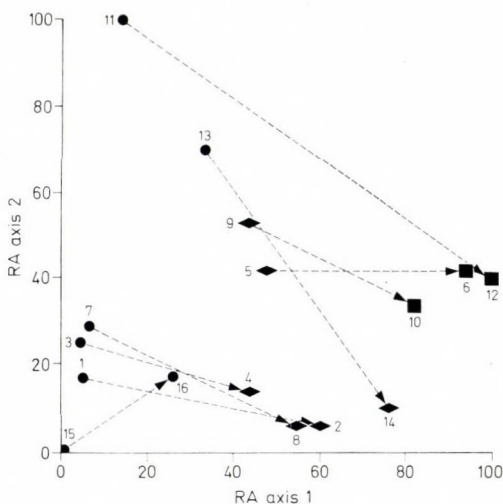



Fig. 1. The RA ordination of relevés. Numbers at symbols are relevé numbers as in Table 1. Arrows connect relevés taken from the same site at an earlier and a later stage. The *Elatini-Eleocharition ovatae* (●) communities (*Cypero-Juncetum* and *Dichostylidi-Gnaphalietum*) are transformed partly to *Bidentetalia* (◆) (which contain elements of *Bidention tripartitae* and *Chenopodion rubri*) and partly to *Bidention tripartitae* (■) associations

Relevés showing an earlier and a more recent state of vegetation in the same site are found in adjacent columns of Table 1. The W_i values calculated from the dominance and characteristic indicator values for each community, and the ordination results are summarized in Table 2.

Ordination, and determination of $f(x)$

Since many species occurred only in very few relevés, the ordination is restricted to the 22 most common species.

An important features of RA is that a high proportion of the total variance is explained by the first axis, whereas the subsequent axes provide relatively little information (cf. GAUCH, WHITTAKER and WENTWORTH 1977). Therefore, when determining the $A = f(x)$ relationship, the loadings of relevés on axis 1 are sufficient (Fig. 1).

In CFA ordinations, the variance of the data is usually more evenly distributed among the axes, and more axes must be considered for the determination of $f(x)$. Before proceeding with the calculations, some assumptions should be made to justify the rejection of further

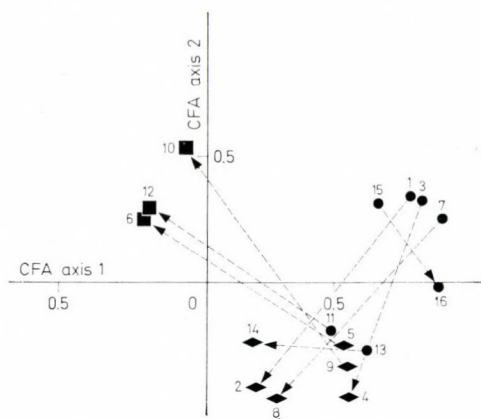



Fig. 2. The CFA ordination of relevés. Symbols correspond to those used in Fig. 1.

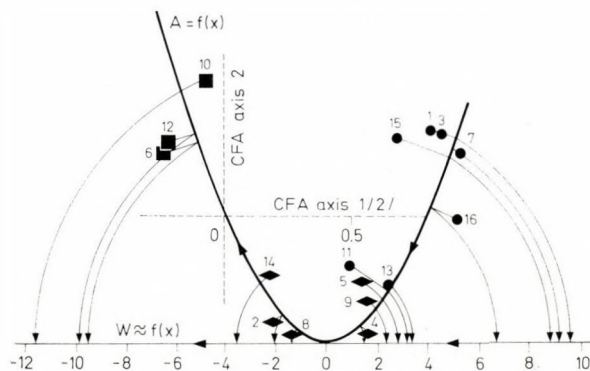



Fig. 3. Approximation to the f(x) values using the CFA ordination. The coenological and hydroecological changes take place along the "A" curve. See text for explanation

axes: the relevant information is carried by the statistically evaluated axes (the percentage variances give only approximate information in this regard), and because of the linearity constraint the relevant information is approximately equally distributed among the axes evaluated. In a more exact analysis, departures from the above assumptions must be taken into account at least within the precision limits of sampling.

The CFA ordination (Fig. 2) shows that the relevés are not positioned along a line which would correspond to the environmental factors. Considering the vegetational changes in the sites examined, the fit to a curve of the ax^n type seems better. The equation obtained by regression (SVÁB 1981), with an arbitrarily selected minimum is

$$A = 2.644\ |(z - 0.4)|\ \exp 1.807 - 0.5.$$

The $f(x)$ values may be determined according to the relative positions of coordinates on the vertical axis which correspond to the relevés. Approximate values may be determined using circles whose center falls to the minimum of A and a line (W) parallel to the horizontal axis as shown in Fig. 3. The distance between points on W approximately equal to those between points on A. The values corresponding to the points of the W line may be considered as a good approximation to $A = f(x)$.

Results

1. The product moment correlation coefficients between the $g(x)$ characteristic indicator values and the $f(x)$ ordination scores are calculated from the data in Table 2. The results are

		f(x)	
		RA	CFA
g(x)	ELLENBERG	.9779	.9289
	ZÓLYOMI	.8642	.8297
	SOÓ	.8419	.8628

2. Based on eq. 2.2 the coefficients of variation are as given below:

V	RA	CFA
ELLENBERG	.1662	.4319
ZÓLYOMI	.2623	.3747
SOÓ	.4775	.4787

In the calculations of V values, the data pairs most contributing to the variance were omitted (MANCZEL 1983). This omission may be substantiated by the T/s test of SACHS (1970). The omitted values belonged to the same pair of objects in both ordinations.

Discussion

1. Statistical methods: The correlation coefficients yielded very high values showing a positive linear relationships between $g(x)$ and $f(x)$. In the evaluation of V values we must consider the fact that in the correlation study

one object is examined at a time; whereas two objects are used when calculating V values, so that the error may be much higher. (That is why the data pair most contributing to the variance is to be omitted.) The V values therefore provide only supplementary information on the relationships.

2. *Ordinations:* The interpretation of ordination results is conditioned upon the thorough knowledged of the characteristics of objects examined. In this paper, the most straightforward interpretation is given for simplicity. I did not consider, for example, the successional differences in the change of object pairs, since the study of these differences may be improved by iterations with the suggested procedure, thus finding several alternatives for $A = f(x)$.

The ordination methods produced quite similar results. Yet, RA seems more useful for starting ordinations because $f(x)$ is more easily determined and the computation of CFA implies subjective decisions. Other ordination methods which give much weight to the first axis, e.g. DCA (Hill and Gauch 1980), may also be used in addition to RA. The V values also support the applicability of RA. The subsequent use of TWINSPAN for modifying indicator values also calls for RA.

3. *Characteristic indicator value systems:* This study is not designed to decide which system is the best, but shows whether the relationships among species regarding an environmental variable are well-reflected by published indicator values. For water requirement, Ellenberg's F-values seem to provide the best description for the species included in this study.

Modification of characteristic indicator values: an example

The aim is to modify Zólyomi's W values, which are generally used in Hungary, to the communities examined such that they more precisely characterize hydroecologically the species of the *Elatini-Eleocharition ovatae Bidention* zone of riverbeds.

Preliminary results are offered by TWINSPAN, whose initial steps may be used with slight modification to decide the extent and direction into which indicator values should be changed. This change must be justified ecologically. Since TWINSPAN starts with an RA ordination of relevés, the extra calculations necessary to these modifications require little effort (Gauch and Whittaker 1981). Table 1 contains the I_j values of species calculated using formula 2.3.

The indicator ability of a species is shown by the absolute value of its I_j score. Of course, I_j gives no information on the environmental variable indicated, thus it is not an indicator value. The "direction" of the environmental factor indicated is determined by the sign if I_j (i.e. wet versus dry). Based on TWINSPAN results, the following conclusions can be drawn: assigning an arbitrary direction to I values, there are three species with high

positive I_j values. These are *Cyperus fuscus* and *Dichostylis micheliana*, character species of the *Nanocyperetalia*, and *Plantago major* ssp. *pleiosperma*, which is a character species of the *Isoëto-Nanojuncetea*. The presence of these species indicates wet environment, therefore they should have high scores in ZÓLYOMI's system. However, species with high negative I_j values should have smaller indicator values in the communities examined. In summary, the following modifications seem indispensable: the indicator value of *Echinochloa crus-galli* should be lowered; its score of nine would be justified if this is an *Oryzion sativae* W. Koch 54 species. In our case this is a *Bidetion* character species. Since $|I_j|$ is high, its decrease with several units is recommended. Because of their high negative I_j values, the indicator values of *Polygonum lapathifolium*, *Bidens tripartita* and *Agrostis stolonifera* also need a change, although less drastic than the value for *Echinochloa crus-galli*. These are *Bidentetea* and *Bidention* character species of the desiccating mud of riverbeds.

I suggest to lower the indicator value of *Echnichloa crus-galli* from 9 to 6 (or possibly to 7 only), that of *Polygonum lapathifolium* and *Bidens tripartita* from 9 to 8, and that of *Agrostis stolonifera* from 8 to 7. These modifications are valied only to the communities mentioned. All the above species are coenologically indifferent (Soó 1964–1980).

The RA results using the modified indicator values are as follows: the correlation coefficient is $r = .9658$, and $V = .1751$ based on all the eight data pairs. For the CFA ordination $r = .8878$. The linear correlations are acceptable even at a value of 7 for *Echinochloa crus-galli* ($r = .9595$). Thus, by the modification of '*W*' indicator values of some coenologically indifferent species, the synphenobiological changes of *Elatini-Eleocharition–Bidention* community types may be more precisely described. The indicator values obtained this way may be applied to similar communities for their hydroecological description.

Summary

Some values of existing characteristic indicator value systems may be modified in order to facilitate a more precise description of communities. The published values represent only a general system within which changes should be implemented, if necessary, considering the basic features of that system. Also, indicator values may be assigned to species not yet included.

The results of such studies may be used in coenosystematic and related surveys (e.g. succession studies, BAGI 1985) and to obtain a more faithful picture on degradation processes. The results may also be useful in a more precise description of the "akoluthia"-space (PRÉCSÉNYI 1985) and in the

determination of mean indicator values characteristic of given community types (cf. Böcher, Kowarik and Bornkamm 1983).

Using the values examined, it is possible to involve other ordination techniques in the search for $A = f(x)$ functions in order to study the performance characteristics of ordinations and to facilitate careful interpretation of ordination results.

ACKNOWLEDGEMENTS

I am grateful to my colleague L. Körmöczi, for the BASIC programs of RA and CFA. I thank Gy. Bodrogközy for his coenological advice, and Prof. I. Précsényi, for his help in preparing the final version of this paper.

REFERENCES

Bagi, I. 1985: Studies on the vegetation dynamics of Nanocyperion communities I. Ordination and characteristic indicator values. *Tiscia (Szeged)* **20:** 29–44.

Bagi, I., Körmöczi, L. 1986: Studies on the vegetation dynamics of Nanocyperion communities II. Classification and ordination of species. *Tiscia (Szeged)* **21:** 13–24.

Bohus, G. 1984: Studies on the pH requirement of soil-inhabiting mushrooms: the R-spectra of mushroom assemblages in deciduous forest communities. *Acta Bot. Hung.* **30:** 155–171.

Böcker, R., Kowarik, I., Bornkamm, R. 1983: Untersuchungen zur Anwendung der Zeigerwerte nach Ellenberg. *Verhandlungen der Gesellschaft für Ökologie* (Festschrift *Ellenberg*) **11:** 35–56.

Ellenberg, H. 1974: Zeigerwerte der Gefäßpflanzen Mitteleuropas. *Scripta Geobotanica* **9.**

Gauch, H. G., Whittaker, R. H. 1981: Hierarchical classification of community data. *J. Ecol.* **69:** 537–557.

Gauch, H. G., Whittaker, R. H., Wentworth, T. R. 1977: A comparative study of reciprocal averaging and other ordination techniques. *J. Ecol.* **65:** 157–174.

Gibson, D. J., Johnson, F. L., Risser, P. G. 1985: Revegetation of unreclaimed coal strip mines in Oklahoma II. Plant communities. *Reclamation and Revegetation Res.* **4:** 31–47.

Hill, M. O. 1973: Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.* **61:** 237–249.

Hill, M. O., Bunce, R. G. H., Shaw, M. W. 1975: Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. *J. Ecol.* **63:** 597–613.

Hill, M. O., Gauch, H. G. 1980: Detrended correspondence analysis: an improved ordination technique. *Vegetatio* **42:** 47–58.

Jahn, W., Vahle, H. 1968: *Die Factoranalyse und ihre Anwendung.* Verlag die Wirtschaft, Berlin.

Juhász-Nagy, P. 1970: Egy operatív ökológia hiánya és szükséglete (Lack and need of an operative ecology). *MTA Biol. Oszt. Közl.* **12:** 441–464.

Juhász-Nagy, P. 1984: *Beszélgetések az ökológiáról* (Conversations about Ecology). Mezőgazdasági Kiadó, Budapest.

Lawley, D. N., Maxwell, A. E. 1963: *Factor Analysis as a Statistical Method.* Butterworths Mathematical Texts, Butterworths London.

Manczel, J. 1983: *Statisztikai Módszerek Alkalmazása a Mezőgazdaságban* (Application of Statistical Methods in Agriculture). Mezőgazdasági Kiadó, Budapest.

Pietsch, W. 1973: Zur Soziologie und Ökologie der Zwergbinsen-Gesellschaften Ungarns (Klasse *Isoëto-Nanojuncetea* Br.-Bl. et Tx. 1943). *Acta Bot. Acad. Sci. Hung.* **19:** 269–288

Précsényi, I. 1981: A növénytársulások struktúrája. (Structure of plant communities.) In: Hortobágyi, T., Simon, T. (eds): *Növényföldrajz, társulástan és ökológia* (Plant Geography, Phytosociology and Ecology). Tankönyvkiadó, Budapest, 202–225.

Précsényi, I. 1986: The akoluthic space and its importance in succession research. *Acta Bot. Hung.* **32:** 53—59.

Sachs, L. 1970: *Statistische Methoden.* Springer, Berlin.

Soó, R. 1964–80: *Synopsis Systematico-Geobotanica Florae Vegetationisque Hungariae.* I–VI. Akadémiai Kiadó, Budapest.

Tímár, L. 1950: A Tiszameder növényzete Szolnok és Szeged között (Les associations végétales du lit de la Tisza de Szolnok á Szeged). *Debreceni Tud. Egyet. Biol. Int. Évk.* **1:** 72–145.

Ujvárosi, M. 1940: Növényszociológiai tanulmányok a Tisza mentén (Phytosociological studies along the Tisza river). *Acta Geobot. Hung.* **3:** 30–41.

Warcholinska, A. U. 1978: Studies on the use of weeds as bioindicators of habitat conditions of agroecosystems. *Ecol. Polska* **26:** 391–408.

Zólyomi, B., Précsényi, I. 1964: Methode zur ökologischen Charakterisierung der Vegetationeinheiten und zum Vergleich der Standorte. *Acta Bot. Hung.* **10:** 377–416.

Zólyomi, B., Baráth, Z., Fekete, G., Jakucs, P., Kárpáti, I., Kárpáti, V., Kovács, M., Máthé, I. 1967: Einreihung von 1400 Arten der ungarischen Flora in ökologische Gruppen nach TW*R*-Zahlen. *Fragmenta Bot.* **4:** 101–142.

Acta Botanica Hungarica 33 (3—4), pp. 211—218 (1987)

STUDIES ON THE COMPETITION BETWEEN *PLANTAGO INDICA* L. AND *SCABIOSA OCHROLEUCA* L.

L. Körmöczi

DEPARTMENT OF BOTANY, JÓZSEF ATTILA UNIVERSITY, SZEGED

(Received: 15 October 1985)

Experiments with replacement series were made with populations of *Plantago indica* L. and *Scabiosa ochroleuca* L. to estimate their competitive relationships. The intraspecific competition within even aged populations of both species was greater than the interspecific competition. In even aged populations the annual *Plantago* proved to be more vigorous competitor than the perennial *Scabiosa*.

The reaction of these species to limitation of water supply was similar. The tolerance of *Plantago indica* was wider than that of *Scabiosa ochroleuca*, whereas the resource utilization was more effective for the latter species at the environmental optimum.

Introduction

Interspecific competition is a deciding factor in the development of plant communities. Insufficient amount of humidity and limited nutrient resources give rise to strong competitive effects (Allen 1982). As a result of an increase in soil moisture content, the biotic potential of coexisting plant species will change; the competitive ability of species may either decrease or increase (Ellenberg 1959, Widera 1980), throwing the populations off their balance. In a study on the balance of two competing species it is basically important to compare the effects of intraspecific and interspecific competition on growth. The relation between them is expressed by the relative crowding coefficient (de Wit 1960), derived from replacement series of mixed populations. This experimental arrangement is especially useful to the study of two interacting species (Harper 1977). Following the analysis of intraspecific behaviour of the annual *Plantago indica* and the perennial *Scabiosa ochroleuca* (Körmöczi 1985), this paper summarizes the results concerning the interspecific competition of these species.

Material and methods

Mixed populations of the two above-mentioned species of psammophilous swards were used in the experiments.

Replacement series (de Wit, 1960) were set up in four plastic boxes (pots) of 30 by 30 by 12 cm size. The ratios of seed numbers were 3 : 0, 2 : 1, 1 : 2, and 0 : 3. In each box 4×9 individuals were grown up. The seeds were sown in a regular tetragonal distribution with 4 cm distance between rows. According to my earlier observations (Körmöczi 1985), the competitive distance of both species was more than 4 cm (4.5 cm for *Plantago indica* and 5.0 cm for *Scabiosa ochroleuca*). To facilitate uniform distribution of sprouting plants, the number of seeds actually sown was twice as much as given above. After sprouting, the extra individuals were of course removed from the pots.

The soil was sand, just like in the former experiments. Until sprouting the moisture content of the soil was 8% in all boxes. Two weeks after sprouting the pots were watered

differently, the daily amount of water being 90, 150, 210 and 270 ml. Thus, by the end of the experiments the soil moisture content was 4%, 7%, 12% and 22%, respectively. These four different cases will be considered as treatment in the sequel.

The individuals were kept in a phytotrone at 20–25 °C with 12 hours long periods of illumination alternating with 12 hours long dark periods. The plants were harvested after 10 weeks. Fresh and dry weights of plants were measured and standardized values of dry weights, the relative yield (RY), were calculated using the formula

$$RY_i = \frac{x_{i,\text{mix}}}{x_{i,\text{pure}}}$$

where

$x_{i,\text{mix}}$ is the total weight of species i in the mixed stand,

$x_{i,\text{pure}}$ is the total weight of species i in a pure population in the replacement series.

The relative yield total (RYT) is obtained as the sum of the two RY values:

$$RYT = RY_1 + RY_2$$

Obviously, the RY and RYT of pure stands will equal 1.0 (DE WIT and VAN DEN BERGH 1965). The departure of RYT from unity reflects the relationship between intraspecific and interspecific effects (HARPER 1977).

The competition between species may be measured by the crowding coefficient of one species relative to the other (RCC). The RCC of *Plantago* to *Scabiosa* will have the form

$$RCC_{P,S} = \frac{\bar{x}_{P,\text{mix}}/\bar{x}_{S,\text{mix}}}{\bar{x}_{P,\text{pure}}/\bar{x}_{S,\text{pure}}}$$

where $\bar{x}_{P,\text{mix}}$ and $\bar{x}_{S,\text{mix}}$ are mean weight of *Plantago* and *Scabiosa*, respectively, in the mixed stands; $\bar{x}_{P,\text{pure}}$ and $\bar{x}_{S,\text{pure}}$ are those for the pure populations in the replacement series (DE WIT 1960).

Table 1

Total yield in pots (x) and average yield ($\bar{x}$) of Scabiosa ochroleuca and Plantago indica at different soil moisture content and relative plant frequency, and the yield of Scabiosa monocultures relative to that of Plantago monocultures ($\bar{x}_S/\bar{x}_P$)

Scabiosa ochroleuca

Soil moisture %	Relative frequency						$\bar{x}_S/\bar{x}_P$
	3 : 0		2 : 1		1 : 2		
	x (mg)	$\bar{x}$ (mg)	x (mg)	$\bar{x}$ (mg)	x (mg)	$\bar{x}$ (mg)	
4	197.8	22.0	145.2	24.2	54.6	18.2	0.6832
7	543.6	60.4	441.6	73.6	162.2	54.1	0.7845
12	862.2	95.8	672.9	112.2	305.8	101.9	1.0692
22	737.0	81.9	595.2	99.2	212.2	70.7	1.0225

Plantago indica

Soil moisture %	Relative frequency					
	3 : 0		2 : 1		1 : 2	
	x (mg)	$\bar{x}$ (mg)	x (mg)	$\bar{x}$ (mg)	x (mg)	$\bar{x}$ (mg)
4	289.7	32.2	189.1	31.5	125.0	41.7
7	692.3	76.9	425.5	70.9	306.7	102.2
12	806.6	89.6	577.3	96.2	381.7	127.2
22	720.6	80.1	451.6	75.3	354.8	118.3

Results

The response of the two species to moisture level changes was similar. On the least wet soil the growth was strongly inhibited, the mean dry weight was only 1/3–1/4 of the maximum dry weight (Table 1). The water level in the individuals was also lowered, being 15–20% less than in the treatment with maximum dry weight (Figure 1). The leaves of *Plantago* individuals turned purple due to the presence of anthocyanines.

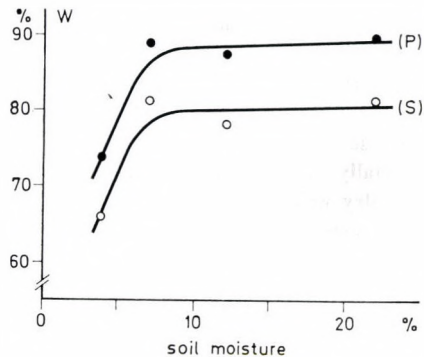



Fig. 1. Relationship between soil moisture and average plant water content (W) of *Plantago indica* (●) and *Scabiosa ochroleuca* (o)

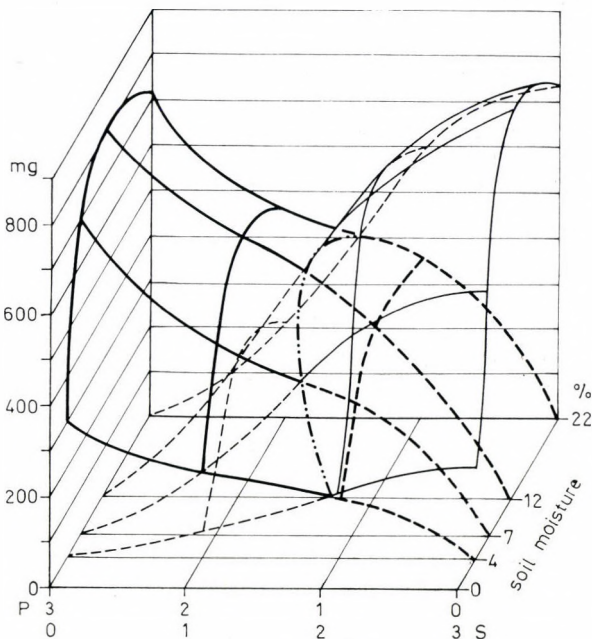



Fig. 2. Relationships of relative plant frequency, soil moisture content and plant dry weight per pot. (Thick lines: *Plantago;* thin lines: *Scabiosa*)

On soils with higher moisture content the development of individuals was faster. The largest dry weight was produced by plants grown in monoculture on soils with 12% moisture content (treatment 3): 95.8 mg/individual for *Scabiosa* and 89.6 mg/individual for *Plantago*. The production of plants on sand with 22% moisture content was also high (85 mg and 88 mg, respectively), but the leaves of *Scabiosa ochroleuca* lost their green colour and turned yellow, owing to the decomposition of chlorophylls. In treatment 4 the decrease of dry weight shows that the moisture content optimum for growth is lower for both species (Figure 2; cf. also ALLEN 1982, WIESE and VAN DIVER 1970).

The relationship between the water content of plants and the soil is shown in Figure 1. There was no significant difference between the three most wet treatments for both species. However, in treatment 1 the water content was much smaller, the difference being about 15%. The change of water content of the two species is similar in the four treatments. Plantago indica has approximately 8% higher water content in all treatments. There is a nearly linear relationship between the increase of mean dry weight and soil moisture at the beginning of the moisture gradient, especially in case of *Scabiosa*.

The proportion of mean dry weight for the individuals grown in monoculture changed in favour of *Scabiosa* along the moisture gradient (Table 1). In the first two treatments, the dry weight of *Plantago* was more than that of *Scabiosa*, although to a small extent in treatment 2. In treatment 3, the dry weight of *Scabiosa* was higher. In all treatments the change of total weight of *Plantago* individuals, as expressed in the function of relative frequency, approximates an inverse sigmoid curve (Fig. 3), which is characterized by an inverse relationship between relative crowding coefficient (RCC) and plant frequency (BERENDSE 1982). The relative crowding coefficient of *Plantago* to *Scabiosa* was the highest in treatment 4. The difference between RCC values for the two mixed series was the highest in treatment 3. The values of relative crowding coefficient are only slightly higher than 1.0 (Table 4). In every

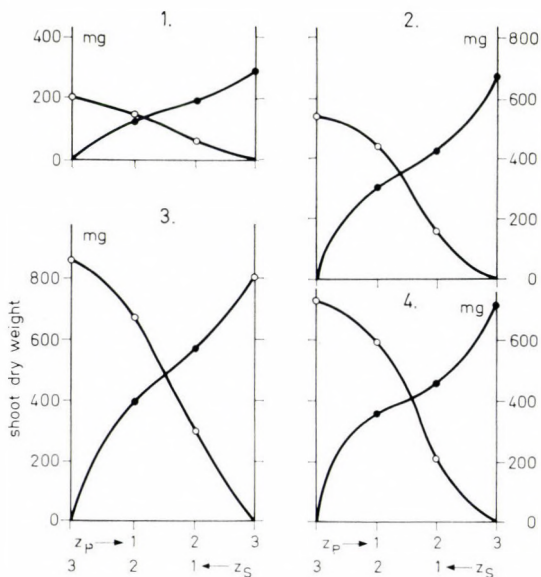



Fig. 3. The shoot dry weight production per pot versus the plant frequency of *Plantago* (z_P) and *Scabiosa* (z_S) at different soil moisture levels: 1. = 4%, 2. = 7%, 3. = 12%, 4. = 22%. ● = Plantago; o = Scabiosa

Table 2

Percentage water content of Scabiosa ochroleuca and Plantago indica at different soil moisture

Scabiosa ochroleuca

Soil moisture %	Relative frequency		
	3 : 0	2 : 1	1 : 2
4	71.3	62.4	63.9
7	80.8	80.7	82.2
12	76.3	78.3	79.7
22	82.8	81.1	80.3

Plantago indica

Soil moisture %	Relative frequency		
	3 : 0	2 : 1	1 : 2
4	70.8	79.3	71.0
7	89.2	88.7	87.9
12	88.7	88.4	85.4
22	90.6	89.0	88.8

Table 3

Relative Yield Total of pots at different soil moisture content

Soil moisture %	Relative frequency (S/P)			
	3 : 0	2 : 1	1 : 2	0 : 3
4	1.0	1.16	0.92	1.0
7	1.0	1.25	0.91	1.0
12	1.0	1.25	1.07	1.0
22	1.0	1.30	0.92	1.0

case, the RCC values pertaining to *Plantago* are higher, indicating that *Plantago* was the stronger competitor in the given situation. (The RCC values of *Scabiosa*, relative to *Plantago*, are the reciprocal values of those for *Plantago*, relative to *Scabiosa*.)

The values of RYT exceeded 1.0 in all the four treatments at low frequency of *Plantago*, and did not reach 1.0 at high frequency (Table 3). In the latter series in treatment 3 (12% soil moisture), RYT was a bit over 1.0. At high *Plantago* frequency the RYT values are similar, except treatment 3, whereas at low frequency RYT increases along with an increase in soil moisture.

Discussion

The experiments were performed to reveal the competitive relationships between coexisting species with different life cycles. The study of the replacement series of the annual *Plantago indica* and the perennial *Scabiosa ochroleuca* suggests that intraspecific competition, as examined earlier (Körmöczi 1985), is stronger in both species than their interspecific competition. Furthermore, the interspecific effect of *Plantago indica* is stronger than that of *Scabiosa ochroleuca* (Figs 4–5).

The competitive effects between populations of the same age were in favour of *Plantago indica*, as shown by the RCC and RYT values. There was no significant difference between treatments in mean weight of *Scabiosa*

ochroleuca, whereas the mean weight of *Plantago indica* measured at low frequency significantly differ from the mean weights obtained either in a monoculture or at al lower frequecy (Table 2, Fig. 4). (The difference between the mean values of *Plantago* in monoculture and at high frequency was not significant.)

The mean weights of *Scabiosa ochroleuca*, although not significant, are higher in every treatment with the proportion of $^2/_3$ than in monoculture. In case of $^1/_3$ proportion, the weights are lower again.

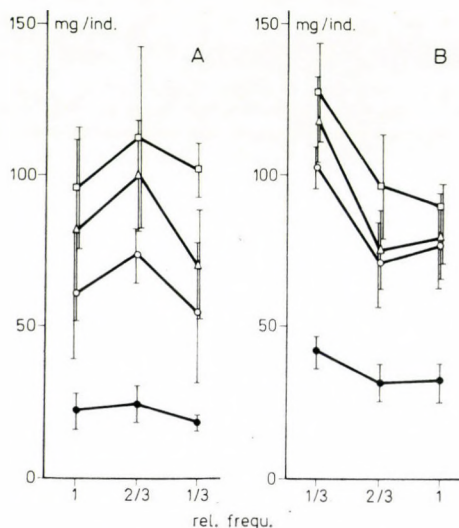



Fig. 4. Relationship between relative plant frequency and average yield at different soil moisture levels. A: *Scabiosa ochroleuca;* B: *Plantago indica.* Soil moisture levels: 4% (●), 7% (o) 12% (□), 22% (△)

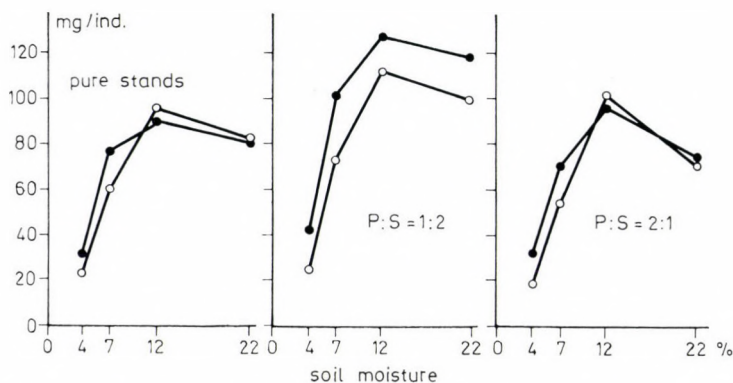



Fig. 5. Relationship between soil moisture content and plant dry weight in pure stands and mixtures of *Plantago* (●) and *Scabiosa* (o)

Table 4

Relative crowding coefficients of Plantago indica with respect to Scabiosa ochroleuca at particular plant frequencies

Soil moisture %	Rel. frequency of *Plantago*	
	1 : 2	2 : 1
4	1.1773	1.1825
7	1.0906	1.0293
12	1.2121	1.0094
22	1.2194	1.0890

Table 5

Significant differences at P % significance levels and significance levels between mean weights in pots of different relative frequencies of Plantago

Soil moisture content: 4%

	2 : 1	3 : 0
1 : 2	9.75 mg 10%	9.12 mg 10%
2 : 1		6.00 mg N. S.

Soil moisture content: 7%

	2 : 1	3 : 0
1 : 2	22.49 mg 5%	20.16 mg 5%
2 : 1		14.52 mg N. S.

Soil moisture content: 12%

	2 : 1	3 : 0
1 : 2	30.16 mg 10%	28.16 mg 10%
2 : 1		16.06 mg N. S.

Soil moisture contentv 22%

	2 : 1	3 : 0
1 : 2	36.01 mg 5%	35.02 mg 5%
2 : 1		13.48 mg N. S.

(*N. S. = not significant; in the case of N. S. the significant difference is given at P % = =10%; all the differences between mean weights of Scabiosa were not significant.*)

The trend in average weight was like above even if soil moisture was sufficient for a maximum growth of *Scabiosa ochroleuca* (treatment 3), and the mean dry weight of this species was higher than that of *Plantago* in monoculture. Note that maximum yield of *Plantago* was produced also in this treatment, but it was higher than the dry weight of *Scabiosa ochroleuca* only at a lower proportion of individuals. High soil moisture resulted in a stress situation for both species, leading to a lower dry weight if compared to treatment 3. However, the mean values increased as the frequency of *Plantago*

decreased even in treatment 4, whereas in case of *Scabiosa* the means first increased and then decreased.

We should consider that the total density of individuals was constant in the monocultures and in the mixed stands. If competition is lacking, and when the interspecific and intraspecific competition are equal for both species, we would expect RYT to be equal to 1.0 and a constant average weight of individuals.

In my experiments the highest average weight of *Plantago* was obtained at the lowest density of this species. This result suggests that the intraspecific effect is stronger than the effect of *Scabiosa* upon *Plantago*. The initial increase of the mean weight of *Scabiosa*, along with the decrease of density, also indicates a strong intraspecific effect. At 1 : 2 proportion of *Scabiosa* and *Plantago* the weight loss of *Scabiosa* is probably due to its decreased density, resulting from intraspecific effects, and to the stronger interspecific effects of *Plantago*. Accordingly, this species, which has a shorter life cycle, may survive in the community by having strong competitive effects on the perennials of the same age. The perennials gain niche space and increase their reproductive capabilities only after the disappearance of *Plantago*.

For the annual species it is essential whether the stronger competitive abilities are maintained even if the competitors are "older" perennials or if the interspecific effects of perennials will dominate.

REFERENCES

Allen, E. B. 1982: Water and nutrient competition between *Salsola kali* and two native grass species (*Agropyron smithii* and *Bouteloua gracilis*). — *Ecology* **63:** 732–741.

Berendse, F. 1982: Competition between plant populations with different rooting depths. III. Field experiments. — *Oecologia* **53:** 50–55.

Ellenberg, H. 1959: Kausale Vegetationskunde und Grünlandwirtschaft. Probleme des Grünlandes. — *Tagungsber. d. Deutsch. Akad. der Landwirtschaftwissenschaften*, Berlin.

Harper, J. L. 1977: *Population Biology of Plants*. Academic Press, London.

Körmöczi, L. 1985: Determination of the degree of intraspecific competition in monocultures. — *Acta Biol. Szeged.* **31:** 173–181.

Szarek, S. R., Smith, S. D., Ryan, R. D. 1982: Moisture stress effects on biomass partitioning in two Sonoran Desert annuals. — *Am. Midl. Nat.* **102:** 338–345.

Widera, M. 1980: The effect of some physical properties of soil and of nitrogen fertilization on intercompetition of species of meadow plants. — *Ekologia Polska* **28:** 525–542.

Wiese, A. F., VanDiver, C. W. 1970: Soil moisture effects on competitive ability of weeds. — *Weed Science* **18:** 518–519.

Wit, C. T. de 1960: On competition. — *Versl. Landbouwk. Onderz.* **66:** 1–82.

Wit, C. T. de, Bergh, J. P. van den 1965: Competition between herbage plants. — *Neth. J. Agric. Sci.* **13:** 212–221.

Acta Botanica Hungarica 33 (3–4), pp. 219–234 (1987)

ECOPHYSIOLOGICAL STUDIES OF THE RELATIONSHIP BETWEEN HEAVY METAL TOXICITY AND NITROGEN NUTRITION IN THE EARLY DEVELOPMENT STAGE OF WINTER WHEAT

FÁBIÁN G.—DÉZSI-DÉVAY M.

UNIVERSITY OF AGRICULTURAL SCIENCES, DEPARTMENT FOR BOTANY AND PLANT PHYSIOLOGY, H-2103 GÖDÖLLŐ
AGRICULTURAL RESEARCH INSTITUTE OF THE HUNGARIAN ACADEMY OF SCIENCES, H-2462 MARTONVÁSÁR

(Received: October 1986)

The toxic effect of some toxic and essential heavy metals on shoot- and root formation in winter wheat in an early development stage of the plants was studied with the aim of finding out whether the nitrogen as a macroelement had any buffering effect on the development of heavy metal toxicity.

In the experiments carried out under controlled conditions in phytotron the action of heavy metals was examined in three groups according the intensity and character of toxicity. The development of the assimilating surface and the root system was least inhibited by the Zn- and Pb treatments. Higher toxicity was caused by the presence of Cd and Ni ions in the nutrient solution. The highest toxic effect on the experimental plants was exercised by Cr^{++} and Cu^{++}.

It was found that in early development stage of the winter wheat the toxic effect of heavy metals could be decreased by an increased level of nitrogen supply. However, this tolerance to heavy metals fundamentally depends on the intensity and character of their toxicity.

The data of the experiments offer help in elaborating a method easy to carry out in practice whereby in the initial stage of development the winter wheat will be able to survive the damaging effect of heavy metals so that the disorders of crop formation can be decreased to minimum.

Introduction

The accumulation of heavy metals in the top soil is increasing in Hungary like anywhere in the world, and in some places developed the heavy metal stress conditions for the cultivated plants.

Besides the usual industrial contaminants and the communication the metal contamination of fertilizers and pesticides (BROWN and JONES 1975, ADDEBSON 1976, WILLIAMS and DAVID 1976) as well as of insufficiently checked sewage sludges (WALLACE and CHA 1977, CHUMBLEY and UNWIN 1982, VALDARES *et al.* 1983, BROWN *et al.* 1983) further increases the heavy metal content in the soil.

The rapid increase in the uptake and toxicity of heavy metals is further promoted by the acidification of the soils (PEICHL 1986) and their deficient organic- and mineral contents, respectively (KIBKHAM 1977, FOY *et al.* 1978).

The general introduction of industrial technologies elaborated with the environment taken into consideration, as well as a decrease in contaminations of traffic- and other origin are expected to take place at a slow rate. So an increasing presence of heavy metals must

be reckoned with for some time in the practice of crop production and ways should be found to prevent or at least reduce the damages. In this respect beside inactivating the heavy metals in the soil, breeding for tolerance to the toxic metal ions and/or controlling the metabolism of the varieties so as to enable the plants to avoid or overcome the toxication may be thought of as well.

Accumulation of toxic heavy metal ions mainly occurs in the upper layer of the soil, so most of the damages they do can be expected in the initial development stage of the plants. The heavy metals when brought into connection with the plant most often act on the growth, the photosynthesis, the respiration and the water balance of all life processes, and they seem likely to exert their primary effect on the membranes (Cseh and Bujtás 1981).

Cadmium equally inhibits the shoot- and root growth of winter wheat (Sommer and Stritersky 1976, Wallace 1977). It is taken up through the leaf and root (Koeppe 1977), and large quantities of it are easily translocated to the shoot (Haghiri 1973, Babich and Stotzky 1978). Of the metabolic processes of plants the photosynthesis and growth are inhibited and the transpiration is reduced by the cadmium (Lamoreaux and Chaney 1978). The Cd inhibits the movement of stomata (Bazzaz *et al.* 1974) and — like other heavy metals — causes disorders of K^+ uptake (Cseh *et al.* 1979). According to Pearson and Kirkham (1981) it changes the water balance and drought tolerance of various wheat varieties.

Lead, like cadmium, is also taken up by the plants through the roots, but only small quantities of it are translocated to the shoot (Zimdaul 1976, Koeppe 1977). The lead, too, inhibits the gremination and slows down the shoot- and root growth of young plants (Carlson et al. 1975, Fábián 1979), and causes disorders in the gas exchange and the movement of stomata (Bazzaz *et al.* 1974). Both the lead (Miles *et al.* 1972) and the cadmium (Hampp *et al.* 1976) prevent the photosynthetic electron transport chainffrom functioning in photosystem II.

According to Cataldo *et al.* (1978) nickel is similarly taken up by the plantsffrom the soil. Temple *et al.* (1981) pointed out that onion, potato, cabbage and lettuce yielded 20–35 per cent less on severely nickel contaminated soil containing 2–3000 ppm Ni. Wallace *et al.* (1977) found that nickel in a quantity of 100 μg/g soil had no toxic effect on maize, while at a concentration of 250 μg/g it decreased the yield. They pointed out that a decrease in the pH of the soil promoted the development of nickel toxication. On a soil containing 1000 μg/g nickel soybean was totally damaged at pH 6.2, while at pH 7.2 the toxicity of Ni lessened. By its translocation from the root the nickel reduced the Fe-, Zn-, Cu- and Mn contents in the soybean plant.

The chrome also disturbs the plant production. Wallace (1977) found the Cr to decrease the yield of beans by some 25 per cent when raised in a culture fluid containing 10^{-5} mol Cr_2O_7. The Cr was translocated to the leaves and shoot as well. Copper and zinc are microelements essential for the mineral nutrition of plants. In hydroponic growth experiments of Cseh and Bujtás (1980) the high Cu^{2+} content inhibited first of all the root growth of the wheat, on the other hand, probably because of the damage caused to the root cells, it was translocated to the shoot in a much lesser extent than the Cd. A 10^{-6} mol concentration of Cu^{2+} still stimulated the root growth of wheat, but $3 \cdot 10^{-6}$ mol caused a 60 per cent inhibition.

The copper decreases the growth of the root better while the cadmium equally acts on the root and the shoot. The absolute quantities of Cu and Cd translocated to the shoot are very different. The complex forming agent added to the culture fluid together with the heavy metal ions prevented the growth inhibition in wheat (Bujtás and Cseh 1981). The copper inhibits the uptake of K^+ by the roots of wheat (Bujtás and Cseh 1982).

According to Wallace *et al.* (1977) and Veltrup (1978) Zn and Cu when in excess in the soil reduces the Fe content of the foliage. Chlorosis could, however, be only observed when the pH value of the soil was low, or when the neutral soil contained very little available

Fe. LÁSZTITY (1982) found the microelement uptake by winter wheat to be the most intensive after tillering. Between the phosphorus content of the soil and the uptake of Zn and Cu a significant correlation was shown.

According to OBERLÄNDER and ROTH (1978) the heavy metals inhibit the K^+ uptake in the following order: Cu, Cd, Cr, Hg, Zn.

VELTRUP (1981) studying the effect of various heavy metals on the uptake of Ca^{2+} established the following order of inhibition: Ni, Co, Cd, Zn, Cu.

In spite of the gradual widening of ecological and ecophysiological investigations concerning the heavy metals our knowledge of the winter wheat, our most important agricultural crop, is deficient. Among others the behaviour of the varieties, or the effect of the macronutrients, e.g. of nitrogen, as regards the development of heavy metal toxicity are not known at all.

Out of the heavy metals non-essential for the plants first of all the undoubtedly toxic cadmium and the less phytotoxic though quantitatively most important lead are deal with in our study. Furthermore, the nickel and chrome, as well as of the essential heavy metals the copper and zink which easily become toxic, were also studied. The effects of the toxic- and of the essential heavy metal ions in excess were evaluated on the basis of the theory of crop formation, by following the changes in the plant productivity. Considering that the damages are expected in the initial phase of development, it was the first stage of crop development, the way the dry matter producing system came into existence that we examined through its two factors: the shoot- and root formation. The assimilation surface was extended as the primary condition of productivity.

The net photosynthetic production which under the influence of heavy metal toxication in an early development stage of the plants.

If by an increase in the intensity of photosynthesis the plants in this early period were helped through the stress caused by the heavy metal ions, the possibility of a yield decrease could supposedly be reduced to minimum.

Material and method

For the experiments two weeks old wheat (*Triticum aestivum* L. cv. Mv 8) plants grown in hydropon were used. The winter wheat MV 8 were obtained from the Wheat Breeding Section of the Agricultural Research Institute of the Hungarian Academy of Sciences.

The seed having swelled for 12 hours at room temperature were germinated in dark thermostat on filter paper wetted with distilled water for 36 hours at 16 °C. During that period the radicle and the coleoptile start developing so that when transferred to the culture pot uniformly germinating seeds can be placed in the holes bored in the covers of the 500 ml vessels. Each vessel was planted with 25 seedlings.

The seedlings were further raised under phytotron conditions, in E 15 chamber. Having been placed in the phytotron they were covered with Petri dishes for 48 hours to decrease the extent of evaporation. The plant material thus prepared was grown for 14 days under conditions of 16-hour daylength, 16 °C temperature and 85% relative humidity. Illumination was provided with CW–GW sources of light at an intensity of 7500 lux.

In the experiments modified Pranyisnyikov solution was used for the nutrition of the plants. Its composition was:

KCl	$1.35 \cdot 10^{-3}$ mol $\cdot$ cm^{-3}
$CaCl_2$	$0.45 \cdot 10^{-3}$ mol $\cdot$ cm^{-3}
$MgSO_4 \cdot 7H_2O$	$0.5 \cdot 10^{-3}$ mol $\cdot$ cm^{-3}
KH_2PO_4	$0.22 \cdot 10^{-3}$ mol $\cdot$ cm^{-3}
$Ca(H_2PO_4)$	$0.77 \cdot 10^{-3}$ mol $\cdot$ cm^{-3}

the microelements were supplied in Hoagland AZ solution (50 ml/1000 ml).

Nitrogen was given in the form of ammonium nitrate at the following concentrations:

NH_4NO_3	10^{-5} mol · dm^{-3}
	$5 \cdot 10^{-5}$ mol · dm^{-3}
	10^{-4} mol · dm^{-3}
	$5 \cdot 10^{-4}$ mol · dm^{-3}
	10^{-3} mol · dm^{-3}
	$5 \cdot 10^{-3}$ mol · dm^{-3}

In the course of preliminary experiments we found that the heavy metal concentrations most suitable for our investigations were between 10^{-5} and 10^{-3} mol. since in that range of concentration changes occurring in the growth of plants can be measured well. The above concentrations of nitrogen were similarly determined after the results of the preliminary experiments.

The heavy metals were introduced in the culture fluid in the form of easily soluble nitrate salts; the amount of nitrogen thus introduced was taken in account when adjusting the nitrogen content of the culture fluids. The pH of the culture fluid supplemented with the heavy metal salts was 5.0–5.2.

The experiments were evaluated on the 14th day after planting. The growth of the plants was characterized by the fresh weight of the shoots and roots and the full assimilatory surface of the shoots. The assimilation surface was measured with an AMM–7 automatic leaf-surface measuring instrument of Japanese make. The total assimilation surface is twice the values obtained with the instrument. For measuring only the living plants were taken into consideration. The data of the replications were evaluated by variance analysis.

Results and Discussion

Changes in the assimilation surface in response to the treatments

Starting from the effect of nitrogen on the intensity of photosynthesis we studied the degree of heavy metal toxicity reached under the influence of ammonium nitrate nutrition.

The primary aim was to lay down the foundations of an agrotechnical method easy to carry out in practice and suitable for lessening the damages of the plants in the initial development stage of the wheat whereby the agronomical yield loss could also be reduced to minimum.

The course of the experiments the growth inhibition of heavy metals, the interaction of various concentrations of heavy metals and ammonium nitrate was evaluated. The results are shown on space lattice diagrams.

On evaluating the effect of Pb added to the culture fluid we found that up to a 10^{-4}-mol concentration of lead the inhibition was low. At various levels of nitrogen it changed, though, but did not exceed 7–15 per cent. Up to the 10^{-4} mol Pb^{2+} concentration the buffering effect of nitrogen on Pb toxication was demonstrable.

With the maximum nitrogen supply — $5 \cdot 10^{-3}$ mol concentration of NH_4NO_1 — the growth of control plants raised over a culture fluid free of Pb exceeded by an average of 40–45 per cent the growth of those not given nitrogen. This effect, as for its proportion, practically remained unchanged at 10^{-4} mol concentration of Pb^{2+}, only the absolute value of the assimilation surface decreased by some 7–10 per cent.

A sharp — about 88–90 per cent — decrease occurred at the $5 \cdot 10\text{M}^4$ mol concentration of Pb. The 10^{-3} mol Pb^{2+} concentration reduced the assimilation surface by an average 95–97 per cent compared to the control. Here the buffering effect of nitrogen was no longer demonstrable (Fig. 1).

The inhibitory effect of Cd was relatively little — about 5–10 per cent — up to the $5 \cdot 10^{-5}$ mol concentration, displaying close similarity to the Ni toxication. However, in the

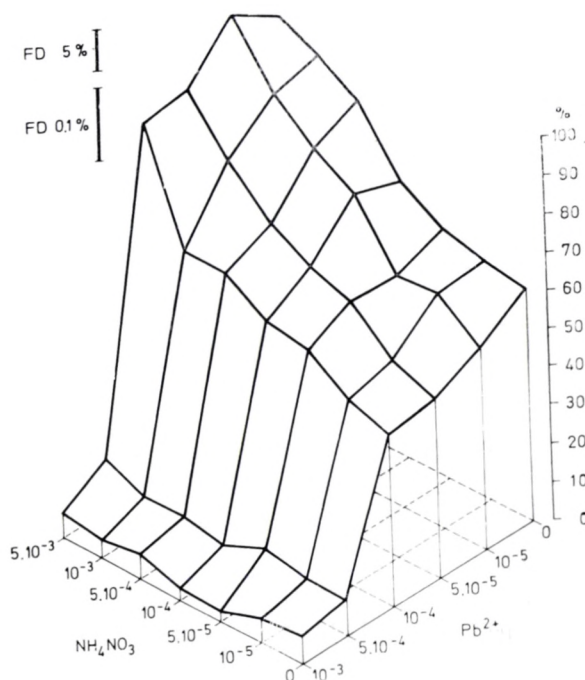



Fig. 1. Joint action of Pb^{2+} ions and NH_4NO_3 on the assimilatory surface of 14-day old winter wheat (Mv-8) seedlings

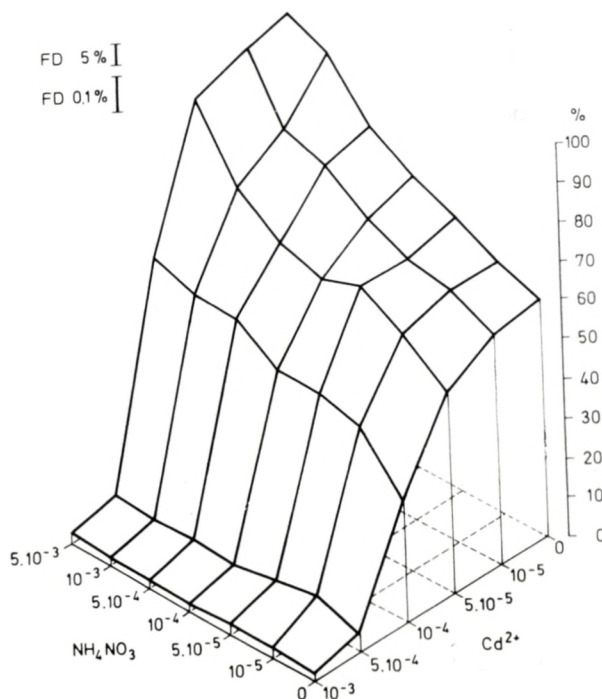



Fig. 2. Joint action of Cd^{2+} ions and NH_4NO_3 on the assimilatory surface of 14-day old winter wheat (Mv-8) seedlings

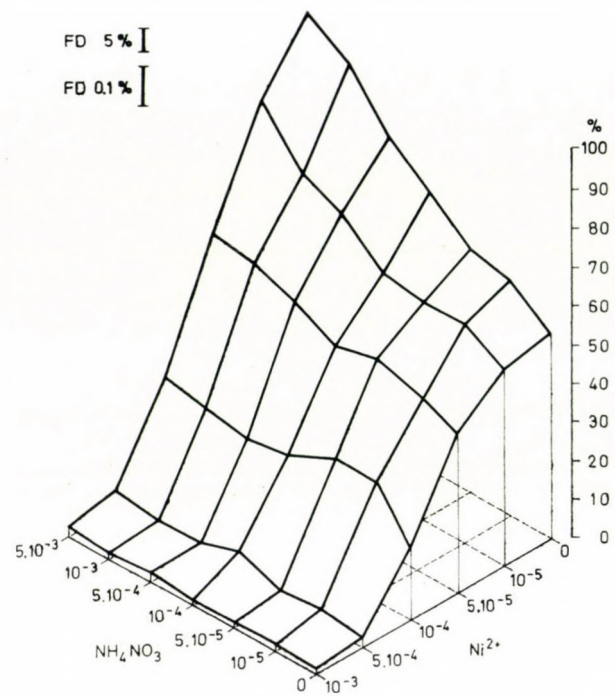



Fig. 3. Joint action of Ni^{2+} ions and NH_4NO_3 on the assimilatory surface of 14-day old winter wheat (v-8) seedlings

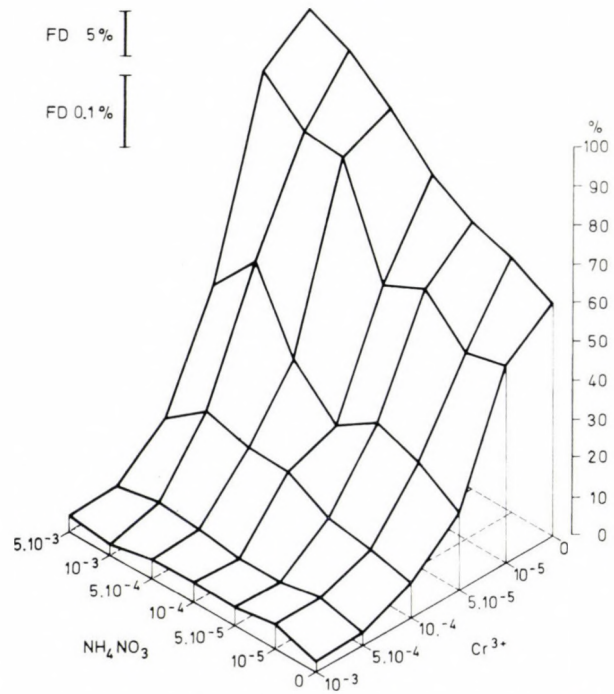



Fig. 4. Joint action of Cr^{3+} ions and NH_4NO_3 on the assimilatory surface of 14-day old winter wheat (Mv-8) seedlings

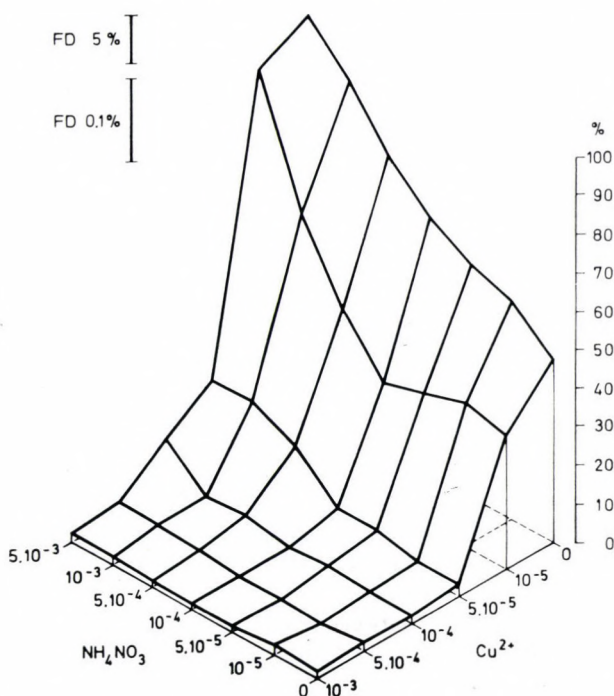



Fig. 5. Joint action of Cu^{2+} ions and NH_4NO_3 on the assimilatory surface of 14-day old winter wheat (Mv-8) seedlings

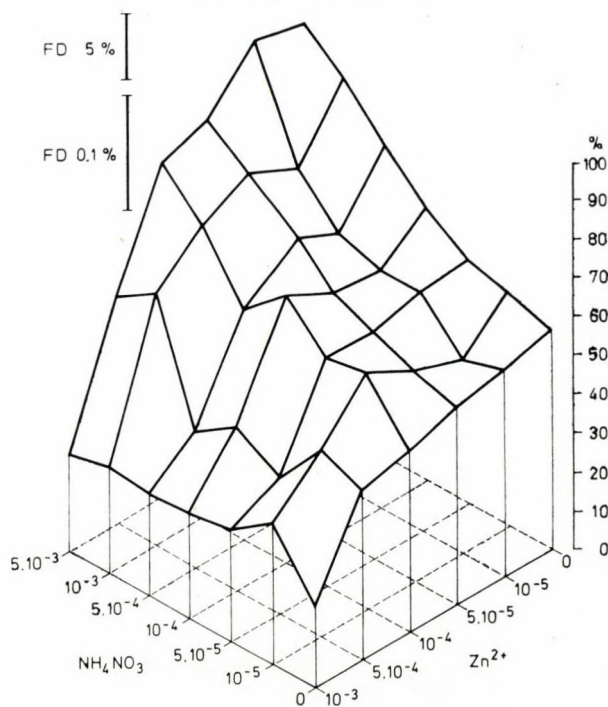



Fig. 6. Joint action of Zn^{2+} ions and NH_4NO_3 on the assimilatory surface of 14-day old winter wheat (Mv-8) seedlings

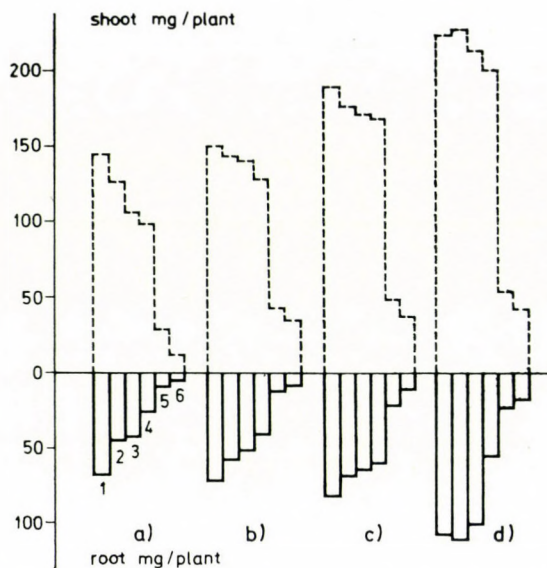



Fig. 7. Effect of Pb^{2+} ions on the shoot- and root growth of 14-day old winter wheat (Mv-8) seedlings at different levels of nitrogen supply (a = 0, b = $5 \cdot 10^{-5}$, c = $5 \cdot 10^{-4}$, d = $5 \cdot 10^{-3}$ mol · dm^{-3} NH_4NO_3). Pb concentrations from left to right: 1 = 0, 2 = 10^{-5}, 3 = $5 \cdot 10^{-5}$, 4 = 10^{-4}, 5 = $5 \cdot 10^{-4}$, 6 = 10^{-3} mol · dm^{-3}. The area of the columns is proportionate with the weight of the plants

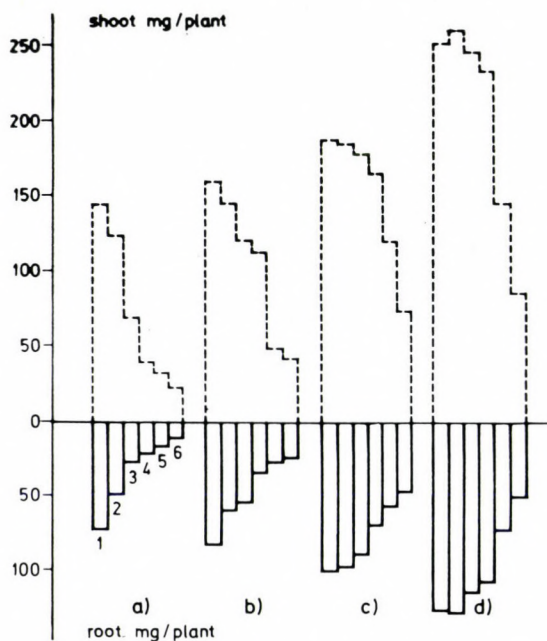



Fig. 8. Effect of Zn^{2+} ions on the shoot- and root growth of 14-day old winter wheat (Mv-8) seedlings at different levels of nitrogen supply (a = 0, b = $5 \cdot 10^{-5}$, c = $5 \cdot 10^{-4}$, d = $5 \cdot 10^{-3}$ mol · dm^{-3} NH_4NO_3). Zn concentration from left to right: 1 = 0, 2 = 10^{-5}, 3 = $5 \cdot 10^{-5}$, 4 = 10^{-4}, 5 = $5 \cdot 10^{-4}$, 6 = 10^{-3} mol · dm^{-3}. The area of the columns is proportionate to the weight of the plant

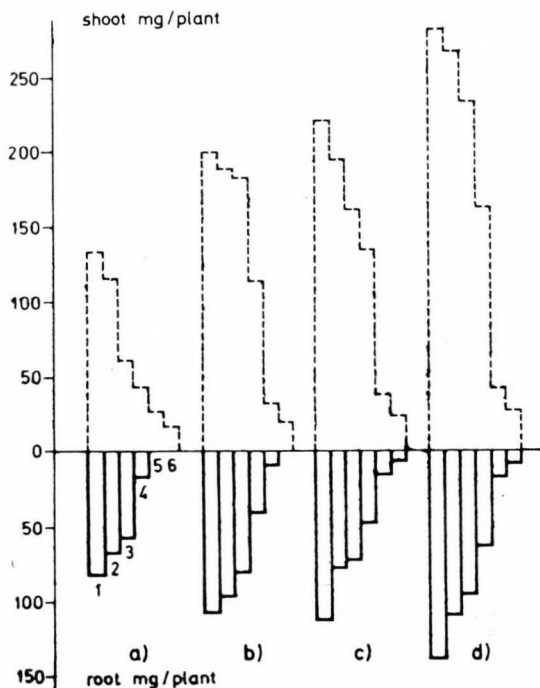



Fig. 9. Effect of Cd^{2+} ions on the shoot- and root growth of 14-day old winter wheat (Mv-8) seedlings at different levels of nitrogen supply (a = 0, b = $5 \cdot 10^{-5}$, c = $5 \cdot 10^{-4}$, d = $5 \cdot 10^{-3}$ mol · dm^{-3} NH_4NO_3). Cd concentration from left to right: 1 = 0, 2 = 10^{-5}, 3 = $5 \cdot 10^{-5}$, 4 = 10^{-4}, 5 = $5 \cdot 10^{-4}$, 6 = 10^{-3} mol · dm^{-3}. The area of the columns is proportionate to the weight of the plant

case of nickel the toxic effect appeared somewhat sooner with the increasing concentration, and at the 10^{-4} mol Ni^{2+} concentration the reduction of the assimilation surface was about 18 per cent more than in the case of cadmium, that is it was almost 50 per cent. At the 10^{-4} mol Cd^{2+} concentration an increase in the nitrogen level still could slow donw the Cd toxication, and an about 25–27 per cent improvement could be achieved, while Ni toxication in the same range of concentration was not practically lessened by the nitrogen. The $5 \cdot 10^{-4}$ and the 10^{-3} mol Cd^{2+}- and Ni^{2+} concentrations almost completely stopped the growth of the shoot (Figs 2 and 3).

Plotting the data of an experiment set up to establish the characteristics of the inhibition caused by Cr^{3+} ions (Fig. 4) gave a typically concave action surface showing a strong inhibition. Under the influence of toxication the assimilation surface began to decrease at the 10^{-5} mol Cr^{3+} concentration, and at the $5 \cdot 10^{-5}$ mol concentration an average reduction of 60–65 per cent was observed. Here a moderating effect of the nitrogen still could be felt. At the $5 \cdot 10^{-3}$ mol NH_4NO_1 level the assimilatory surface was larger by about 6 per cent than in the nitrogen deficient control. At the 10^{-4} mol concentration of Cr^{3+} the nitrogen no longer increased the production (Fig. 4).

The essential Cu^{2+} and Zn^{2+} ions in excess showed differences in the character of toxicity. While the Cu caused strong inhibition very soon, practically at the 10^{-5} mol concentration already (similarly to the Cr toxication) and reduced the assimilatory surface by some 10–25 per cent, the Zn only gradually and slighty reduced the assimilatory surface. Major inhibition

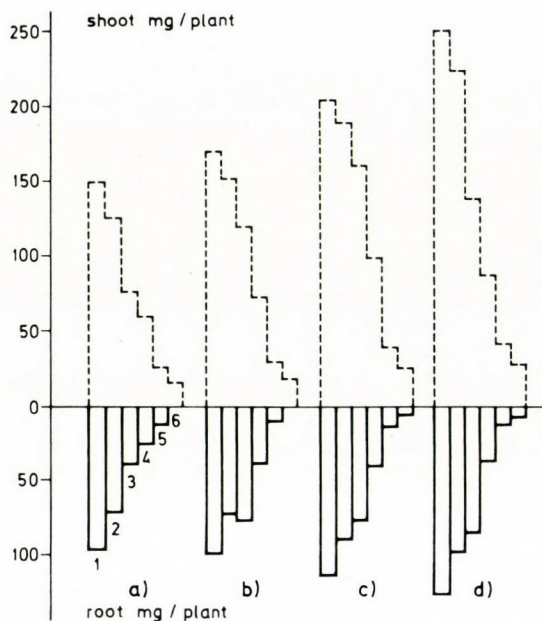



Fig. 10. Effect of Ni^{2+} ions on the shoot- and root growth of 14-day old winter wheat (Mv-8) seedlings at different levels of nitrogen supply (a = 0, b = $5 \cdot 10^{-5}$, c = $5 \cdot 10^{-4}$, d = $5 \cdot 10^{-3}$ mol · dm^{-3} NH_4NO_3). Ni concentration from left to right: 1 = 0, 2 = 10^{-5}, 3 = $5 \cdot 10^{-5}$, 4 = 10^{-4}, 5 = $5 \cdot 10^{-4}$, 6 = 10^{-3} mol · dm^{-3}. The area of the columns is proportionate to the weight of the plant

first appeared at the $5 \cdot 10^{-4}$ mol concentration (Figs 5 and 6). At the $5 \cdot 10^{-5}$ mol concentration the Cu toxication reduced the assimilatory surface by 65–70 per cent. The buffering effect of nitrogen was only slightly felt. Up to the limit of $5 \cdot 10^{-4}$ mol concentration toxication by Zn — like by lead — could be moderated.

According to the results of the experiments the heavy metals examined can be placed in three groups on the basis of the character of toxicity. The shoot growth, that is the assimilatory surface was least reduced by the Zn and Pb. The toxication exhibited a striking similarity in character. The toxications caused by Cd and Ni were nearly the same in intensity and character, though of much greater extent than in the case of Zn and Pb. Cr and Cu possessed the strongest toxic effect; their curves of character show almost the same descent.

With an improvement in the nitrogen supply the toxic effect of heavy metals generally could be moderated up to the limit of 10^{-4} mol concentration. In the case of Zn, however, toxication even at the $5 \cdot 10^{-4}$ mol concentration could be further lessened by some 20–22 per cent. The reducing effect of Cr and Cu on the surface of photosynthesis could be controlled in any considerable measure by nitrogen supply only to the limit of 10^{-5} mol concentration.

Growth response of roots to the treatments

The growth of the root system was studied simultaneously with the measuring of the assimilatory surface. The characteristics of the effect of heavy metals, the differences in inhibition were followed by measuring the fresh weight of the root and determining the ratio of root to shoot.

The measuring data unequivocally showed that the heavy metals exercised a very strong inhibitory effect on the root growth.

The roots showed characteristic changes. In the case of a severe toxication the radicle completely stopped growing, sometimes after developing some weak and short protrusions. A further typical symptom of the severe toxication was the hook-like bending of the root tips of some roots. In that tecaeh root system fell far behind the control both in weight and length owing to its brush-like growth. A mild toxication generally caused some minor decrease in the weight of the root system only.

The growth of the roots was examined in close connection with that of the shoots, since we found that in response to heavy metal toxication the ratio of shoots to roots changed. So, for the sake of better demonstration we plotted the growth of shoots and roots together.

The growth of roots was least inhibited by the Pb^{2+} and Zn^{2+} ions. As seen in Figs 7 and 8 any considerable reduction only occurred at the very high $5 \cdot 10^{-4}$ mol concentration, and the shoot/root ratio did not practically change. In an interesting way at low concentrations both heavy metals slightly stimulated the growth of roots.

According to the data of measuring Ni^{2+} and Cd^{2+} even at a low — 10^{-4} mol — concentration caused serious damage to the roots. Inhibition by Ni was somewhat greater. Nitrogen deficiency increased the destruction of roots. At the $5 \cdot 10^{-3}$ mol concentration of NH_4NO_1 the reduction of shoots was 6–93 and that of roots 23–96 per cent with the Cd^{2+} concentration increased from 10^{-5} to 10^{-3} mol. An increase in the concentration of Ni^{2+} caused 4–94 per

shoot mg / plant
250
200
150
100
50
0
50
100
150
1 2 3 4 5 6
a) b) c) d)
root mg / plant

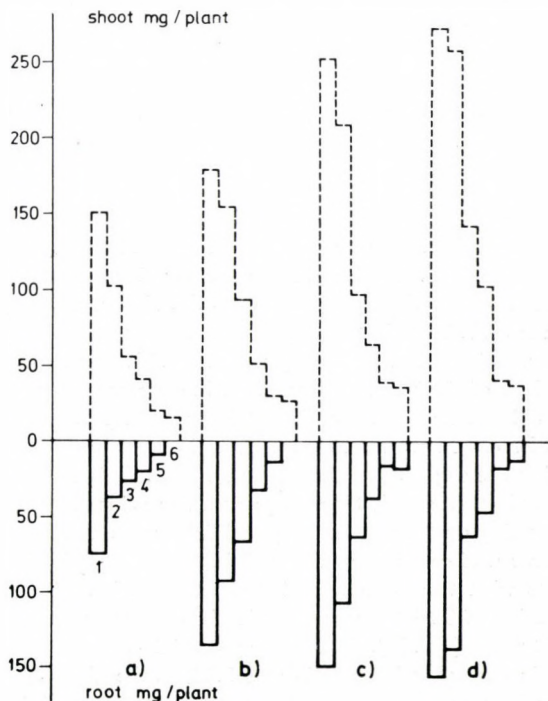



Fig. 11. Effect of Cr^{3+} ions on the shoot- and root growth of 14-day old winter wheat (Mv-8) seedlings at different levels of nitrogen supply (a = 0, b = $5 \cdot 10^{-5}$, c = $5 \cdot 10^{-4}$, d = $5 \cdot 10^{-3}$ mol · dm^{-3} NH_4NO_3). Cr concentration from left to right: 1 = 0, 2 = 10^{-5}, 3 = $5 \cdot 10^{-5}$, 4 = 10^{-4}, 5 = $5 \cdot 10^{-4}$, 6 = 10^{-3} mol · dm^{-3}. The area of the columns is proportionate to the weight of the plant

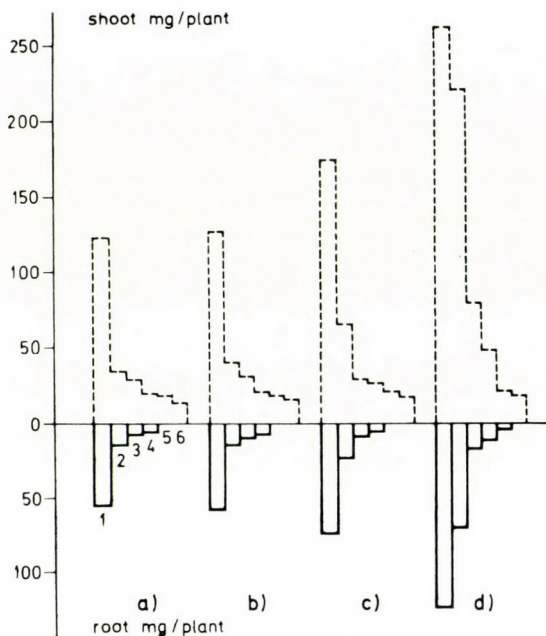



Fig. 12. Effect of Cu^{2+} ions on the shoot- and root growth of 14-day old winter wheat (Mv-8) seedlings at different levels of nitrogen supply (a = 0, b = $5 \cdot 10^{-5}$, c = $5 \cdot 10^{-4}$, d = $5 \cdot 10^{-3}$ mol · dm^{-3} NH_4NO_3). Cu concentration from left to right: 1 = 0, 2 = 10^{-5}, 3 = $5 \cdot 10^{-5}$, 4 = 10^{-4}, 5 = $5 \cdot 10^{-4}$, 6 = 10^{-3} mol · dm^{-3}. The area of the columns is proportionate to the weight of the plant

cent inhibition to shoots and 34–96 per cent inhibition to roots (Figs 9 and 10). The shoot/root ratio of the control plants raised over a culture fluid free of metal was 2.03 on the average of the experiments. On the other hand, increasing concentrations of Cd^{2+} and Ni^{2+} did greater damage to the roots than to the shoots, and towards the highest concentrations of them the shoot/root ratio became 3.17. The absence of nitrogen decreased the growth of the plants to a considerable extent and increased the heavy metal sensitivity of the roots. High — 10^{-4} to 10^{-3} — concentrations of Cd^{2+} and Ni^{2+} resulted in a serious damage or even destruction of the roots. Between the lowest and the highest heavy metal concentrations the intensity of inhibition could be lessened to some extent with an increase in the nitrogen supply.

The roots suffered the greatest damage under the influence of Cr^{3+} and Cu^{2+} ions. Even with a maximum nitrogen supply the root growth was reduced by 2–94, the shoot growth by 5–88 per cent depending on the concentration of Cr^{3+} compared to the control. The roots of the plants raised over a nitrogen-free culture fluid suffered considerable damages, as seen in Fig. 11. Treatments with Cu^{2+} also caused a great reduction of root growth. From the $5 \cdot 10^{-5}$ mol concentration of Cu^{2+} the roots practically stopped growing and died irrespective of the nitrogen concentration (Fig. 12). Both in the case of Cr- and Cu toxication the shoot/root ratio changed. While in the control this ratio was 2.13, at the highest Cr^{3+} concentration it changed to 3.76 even with an optimum nitrogen supply. In the case of Cu the shoot/root ratio shifted further in favour of the shoots because of the serious destruction of roots. The Cu^{2+} toxicity could only slightly be counterbalanced with an improvement in the nitrogen supply.

Since it was mentioned in the section "Material and method" that only living plants were taken into consideration for measuring, it is worth speaking briefly of the mortality

occurring in response to heavy metal toxication. The mortality percentage of seedlings considerably increased with the rising concentrations of heavy metals. In the control treatments (concerning all experiments) the proportion of destroyed plants was 6–8 per cent. Injuries caused during transplantation to the culture pots probably had some part in this.

In the $5 \cdot 10^{-5}$ and 10^{-4} mol range of concentration mortality caused by the heavy metals examined, reduced by the extent of destruction found in the control, was about 18–20 per cent. The 10^{-3} mol heavy metal concentration resulted in some 50 per cent destruction of seedlings. Cr and Cu caused a destruction higher than that — 65–70 per cent on an average.

The symptoms formed two characteristic groups. On the one hand, at very high metal concentrations the seedlings stopped growing almost immediately after transplantation to the cultura pots; on the other hand, at lower concentrations the seedling withered after a few days offgrowing.

Summing up our results concerning the joint effect of heavy metals and nitrogen supply on the basis of the growth of shoot (assimilatory surface) and root we can establish the fact that the rising nitrogen content of the culture fluid had a favourable effect on the heavy metal tolerance of the plants. With an increase in the NH_4NO_3 level the development of toxicity and first of all the damage of shoots could be delayed to an extent depending on the heavy metal concentration. The results are summed up in Fig. 13 where the damages of nitrogen deficient plants and of those raised with an optimum nitrogen supply can be seen. The figure clearly show the character of the toxic effect of heavy metals, and the difference in production due to the action of nitrogen against the influence of heavy metals.

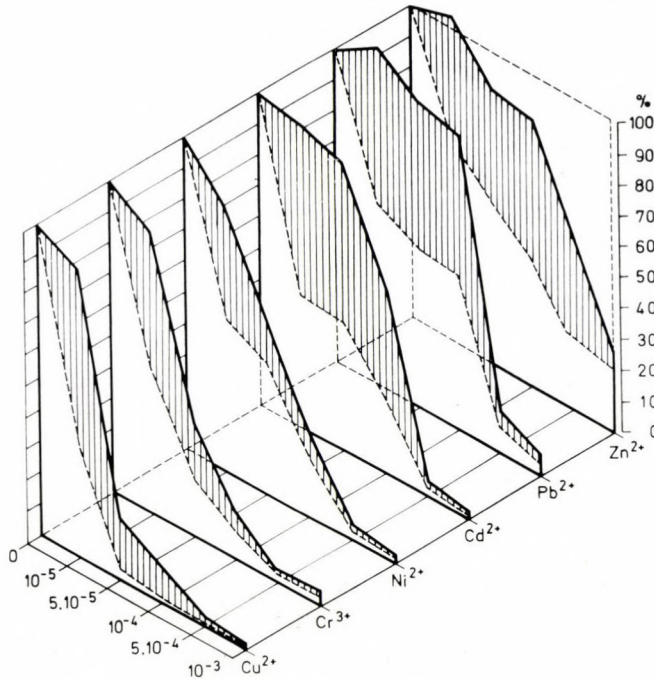



Fig. 13. Characteristic curves of the toxic effects of heavy metals without nitrogen and with optimum nitrogen supply. The striped area shows the effect of nitrogen. N deficiency (- - - -), optimum N supply (———)

Summary

The accumulation of heavy metals in the soils and the strengthening of factors promoting the development of plant toxications increasingly call attention to the necessity of studying the reactions of cultivated plants.

The excessive metal contamination of soils may influence the photosynthetic production and hinder the development of yield components.

The general introduction of industrial technologies that spare the environment, and the reduction of contaminations of traffic- and other origin are expected to take place at a slow pace. For that reason the increasing presence of heavy metals must for a rather long time be reckoned with in the practice of crop production, and ways must be found to prevent or lessen the damages. Parallel to inactivating the heavy metals in the soil we may try breeding for tolerance to toxic metal ions, and/or controlloing the metabolism of plants so as to enable them to avoid or overcome the toxication.

In the early development phase of the plant the decreasing netto photosynthetic production reduces the biological and agronomical production through an increase in the amount of dry matter.

If by an incresse in the intensity of photosynthesis the plants in this early period were helped through the stress caused by the heavy metal ions, the possibility of yield reduction could supposedly be reduced to minimum.

In the course of our work we started from the stimulatory effect of the nitrogen on the intensity of photosynthesis, and studied the influence of nitrate nutrition on heavy metal toxicity in an early development phase of winter wheat. Of the heavy metals non-essential for plants the definitely toxic cadmium and the less phytotoxic but quantitatively highly important lead were dealt with, furthermore the nickel and chrome, and of the essential heavy metals the copper and zinc were also examined for their effect on the growth of shoot (assimilatory surface) and root.

In our hydroponic experiments the 14 days old winter wheat (Mv 8) seedlings suffered strong heavy metal toxication increasing with the latter's concentration. From the point of view of toxicity the heavy metals could be placed in three groups.

The least toxic effect was exercised by Zn and Pb on the experimental plants. The inhibition caused by the two metals was of the same character An almost equally greater inhibition was caused by Cd and Ni. The greatest effects similar in character were exercised by Cr and Cu.

The results of the experiments showed that under the influence of nitrogen nutrition carried out with ammonium nitrate the resistance of the plants improved. It was found, however, that the nitrogen made its effect felt only to a certain limit. In the case of Zn and Pb the increased nitrogen supply reduced the toxic effect up to the 10^{-4} mol heavy metal concentration.

Reduction of the shoot- and root wieght caused by Cd and Ni could only be moderated to the limit of $5 \cdot 10^{-5}$ mol concentration. Toxication by Cu and Cr, and the other hand, could but slightly be lessened with the increased nitrogen level even at the lowest 10^{-5} mol concentration.

Our results seem to support the theory that with an improvement in the nitrogen in an early development stage of the plants the harmful effect of heavy metals can be decreased.

The elaboration of details, the disclosure of correlations naturally required further investigations.

ACKNOWLEDGEMENTS

The authors are indebted to Mrs. Piroska HORVÁTH-ANGYAL and Mr. János BILIK for their technical assistance during the experiments.

REFERENCES

Andersson, A. 1976: On the influence of manure and fertilizers on the distribution and amounts of plant-available Cd in soils. *Swedish J. Agric. Res.* **6:** 27–36.

Babich, H., Stotzky, G. 1978: Effects of cadmium on the biota. *Adv. Applied Microbiol.* **23:** 55–117.

Bazzaz, F. A., Carlson, R. W., Rolfe, G. L. 1974: The effect of heavy metals on plants. I. Inhibition of gas exchange in sunflower by Pb, Cd, Ni, and Tl. *Environ. Pollut.* **7:** 241–246.

Brown, J. C., Jones, W. E., 1975: Heavymetal toxicity in plants. 1. A crisis in embryo. *Communs. Soil Sci. Pl. Analysis.* New York **6.**/ 4: 421–438.

Brown, K. W., Thomas, J. C., Slowey, J. F. 1983: The movement of metals applied to soils in sewage effluent. *Water, Air and Soil Pollution.* **19:** 43–54.

Bujtás, C., Cseh, E. 1981: Effect of heavy metals and chelating agents on potassium uptake of cereal roots. *Plant and Soil* **63:** 97–100.

Bujtás K., Cseh, E. 1982: Réz hatása a búzagyökerek K^+ felvételi rendszerére (Effect of copper on the system of K^+ uptake by wheat roots). *MTA Biol. Oszt. Közl.* **25:** 609–622.

Carlson, R. W., Bazzaz, F. A., Rolfe, G. L. 1975: The effect of heavy metals on plants: Part II. Net photosynthesis and transpiration of whole corn and sunflower plants treated with Pb, Cd, Ni and Tl. *Environ. Res.* **10:** 113–120.

Cataldo, D. A., Garland, T. R., Wildung, R. E. 1978: Nickel in plants. *Plant Physiol.* **62:** 563–565.

Chumbley, C. G., Unwin, R. J. 1982: Cadmium and lead content of vegetable crops grown on land with a history of sewage sludge application. *Environmental Pollut.* (Series B) **4:** 231–237.

Cseh, E., Bujtás, K., Szabados, M. 1979: Preliminary notes about the ffects of heavy metals on plant nutrition. *Proc. First Intern. Symp. on Plant Nutrition*, Varna Bulgaria, **2:** 315–319.

Cseh, E., Bujtás, K. 1980: Effects of heavy metals on growth and K^+ absorption of wheat. *Proc. 20th. Hung. Ann. Meet. Biochem.*, 233–234.

Cseh E., Bujtás K. 1981: Környezet-szennyezés: nyomelem toxicitás (Environment pollution: trace element toxicity). *MTA Biol. Oszt. Közl.* **24:** 247–258.

Fábián Gy. 1979: Szántóföldi növények érzékenysége ólomvegyületekre, különös tekintettel a klorofill tartalom alakulására (Sensitivity of field crops to lead compounds, with special regard to changes in the chlorophyll content). Egyet. dokt. ért. Agrártud. Egyet. Gödöllő.

Foy, C. D., Chaney, R. L., White, M. C. 1978: The physiology of metal, toxicity in plants. *Ann. Rev. Plant Physiol.* **29:** 511–566.

Haghiri, F. 1973: Cadmium uptake by plants. *J. environ. Qual.*, **2:** 93–96.

Hampp, R., Heuligh, K., Ziegler, H. 1976: Effects of zine and cadmium on photosynthetic CO_2-fixation and Hill activity of isolated spinach chloroplasts. *Z. Pflanzenphysiol.* **77:** 336–344.

Kirkham, M. B. 1977: Organic matter and heavy metal uptake. *Compost Sci.*, Emmaus, **18.** / 1: 18–21.
Koeppe, D. E. 1977: The uptake, distribution, and effect of cadmium and lead in plants. *The Science of the Total Environment.* **7:** 197–206.
Lamoreaux, R. J., Chaney, W. R. 1978: The effect of cadmium on net photosynthesis, transpiration, and dark respiration of excised silver maple leaves. *Physiol. Plant.* **43:** 321–326.
Lásztity, B. 1984: Connection between the nutrient uptake of winter wheat and the level of nutrient supply of the soil. *Proc.* **9.** *Int. Pl. Nutr.*, Warwick, **1:** 316.
Miles, C. D., Brandle, J. R., Daniel, D. J., Chu-Der, O., Share, P. D., Uhlik, D. J. 1972: Inhibition of photosystem II. in isolated chloroplasts by lead. *Plant Physiol.* **49:** 820–825.
Oberländer, H. E., Roth, K. 1978: Die Wirkung der Schwermetalle Chrom, Nickel, Kupfer, Zink Cadmium, Auecksilber und Blei auf die Aufnahme und Verlagerung von Kalium und Phosphat bei jungen Gerstenpflanzen. *Z. Pflanzenernahr. Bodenkd.* **141:** 107–116.
Pearson, C. H., Kirkham, M. B. 1981: Walter relations of Wheat cultivars grown with cadmium. *J. of Plant Nutrition,* **3:** 309–318.
Peichl, R. 1986: A mezőgazdaságilag hasznosított talajok elsavanyodása. Melioráció, öntözés és tápanyaggazdálkodás (Acidification of agriculturally utilized soils. Melioration, irrigation and nutrient management). **1:** 71–80. AGROINFORM, Budapest.
Sommer, G., Stritersky, A. 1981: Gefässversuche zur Ermittlung der Schadgrenzen von Cadmium, Kupfer, Blei und Zink im Hinblick auf den Einsatz von Abfallstoffen in der Landwirtschaft. *Landw. Forsch.*, Frankfurt/M. ,**29:** 88–100.
Temple, P. J., Bisessar, S. 1981: Uptake and toxicity of nickel and other metals in crops grown on soil contaminated by a nickel, refinery. *Journ. of Plant Nutr.*, **3:** 473–482.
Valdares, J. M. A. S., Gal, M., Mingelgrin, U., Page, A. L. 1983: Some heavy metals in soils treated with sewage sludge, their effects on yield, and their uptake by plants. *J. Environ. Qual.*, **12:** no. 1.
Veltrup, W. 1978: Characteristics of zinc uptake by barley roots. *Physiol. Plant.* **42:** 190–194.
Veltrup, W. 1981: Effect of heavy metals on the calcium absorption by intact barley roots. *Journ. of Plant Nutr.* **3:** 225–231.
sources. *Journal Air Pollut.* **26**(7): 655–666.
Wallace, A. 1977: Trace metal uptake, concentration, cobalt, copper, nickel, zinc, cadmium. *Commun. in Soil and Plant Analysis,* **8**(9): 689–691.
Wallace, A., Alexander, G. V., Chaudry, F. M. 1977: Phytotoxicity of cobalt, vanadium, titanium, silver, and chromium. *Commun. in Soil Science and Plant Analysis,* **8(9):** 751–756.
Wallace, A., Romney, E. M., Alexander, G. V., Kinnear, J. 1977: Phytotoxicity and some interactions of the essential trace metals iron, manganese, molybdenum, zinc, copper, and boron. *Commun. in Soil Science and Plant Analysis,* **8**(9): 741–750.
Wallace, A., Cha, J. W. 1977: Trace metals in two garden products derived from sewage sludge. *Commun. in Soil Science and Plant Analysis,* **8**(9): 819–821.
Wallace, A., Romney, E. M., Cha, J. W., Soufi, S. M., Chaudhry, F. M. 1977: Nickel, heavy metal toxicity, chelating agents, soil pH, iron chlorosis, spectographic analysis. *Commun, in Soil Science and Plant Analysis,* **8**(9): 754–764.
Wallace, A., Romney, E. M., Alexander, G. V., Soufi, S. M. 1977: Some interactions of cadmium with other elements in plants. *Commun. in Soil Science and Plant Analysis.* **8**(9): 765–772.
Williams, C. H., David, D. J. 1976: The accumulation in soil of cadmium residues from phosphate fertilizers and their effect on the cadmium content of plants. *Soil Science,* Baltimore, **121** (2): 86–93.

Acta Botanica Hungarica 33 (3—4), pp. 235—237 (1987)

THE INFLUENCE OF CU^{2+} AND pH ON THE MUTAGENIC EFFECT OF ETHYLENIMINE AND ON CHROMOSOME ABERRATIONS IN BARLEY

T. PUSZTAI

INSTITUTE OF ECOLOGY AND BOTANY HUNGARIAN ACADEMY OF SCIENCES VÁCRÁTÓT, HUNGARY

(Received: 1 September 1987)

Experiments were made for finding out the action of ethylenimine (EI) in the presence of Cu^{2+} ions on chromosome aberration frequency of barley seeds at several pH values. Chromosomal aberrations were detected at metaphase. The results indicate that there is a considerable increase in frequency of aberrations in line of copper ion concentration and pH. At an alkaline pH (7.8) this frequency was 2.5 times lower than at an acidic pH value (5.6).

Copper treatment following incubation of seeds with EI did not resulted in higher number of aberrations. The treatmrnt of barley seeds with EI combined with copper, which is non-mutagenic by itself, causes an enhance of chromosome aberrations depending on pH of the media. We presume that copper ion is an inhibitor for repair enzymes, and that is why it can be a dangerous pollutant of environment.

Introduction

Ethylenimine (EI) is reported as an effective alkylating mutagen, as well as in plants (NILAN *et al.*, 1964). Variation in experimental conditions is known to modify the observed effect of EI and of other chemical mutagens (KONZAK *et al.*, 1964). E.G. the mutagenic effect of EMS increases in the presence of copper and zinc ions on *Crepis capillaris* seeds (GRINICH 1981).

The aim of this work is to establish the effectiveness of EI onto chromosomal aberrations in barley seeds, at various pH values and copper concentrations.

Material and Methods

For the cytological test a Hungarian barley strain, Mv 43 (2n = 14) was used. The concentrations of ingredients were determined in preliminary tests. We worked with 10^{-3}, 10^{-4} and 10^{-5} M $CuSO_4$ solutions in bi-distilled water. The concentration of EI was 2.3×10^{-3} M.

In the combined experiments seeds were soaked for 3 hours at 24 ± 0.5 °C in phosphate buffer at several concentrations of $CuSO_4$ solution at pH 5.6, 7.0, 7.8. These are altogether twelwe combination with EI.

When the Cu^{2+} treatment was applied next to EI, seeds were soaked in EI solution for three hours, washed in twice distilled water and embedded in copper sulphate solution of different concentrations for another 3 hours. Cytological investigations were made as before (PUSZTAI and VÉGH, 1978).

Results and Discussion

Cytological effects of EI depending on concentration of synchronously applied Cu^{2+} and pH changes are shown on Fig. 1. There is a considerable increase of frequency of chromosome aberrations in line with higher copper concentration and pH.

10^{-4} M Cu^{2+} at pH = 5.6 was the most effective, it reached as high as $25.03 \pm 2.19\%$. Additional, ten times Cu^{2+} increase at the same pH resulted in 2.3 times decrease number of aberrations. Under the same EI concentration the frequency of aberrations enhances until 10^{-4} M Cu^{2+}: at pH = 5.6 it grows for 3.9 times and at pH = 7.8 for 1.8 times. Consequently at alkalic pH the frequency of aberrations was 2.5 times lower.

As it can be seen on Table 1, copper seed treatment after EI incubation did not change the aberration number.

Without any other mutagenic treatment copper caused very little alterations, that is why we should ascribe the increased frequency of aberrations to EI activity, not to a joint effect of EI and Cu^{2+}.

During studies of copper-stimulated chromosome aberrations, J. Moutschen-Dahmen and M. Moutschen-Dahmen obtained a maximal effect, with

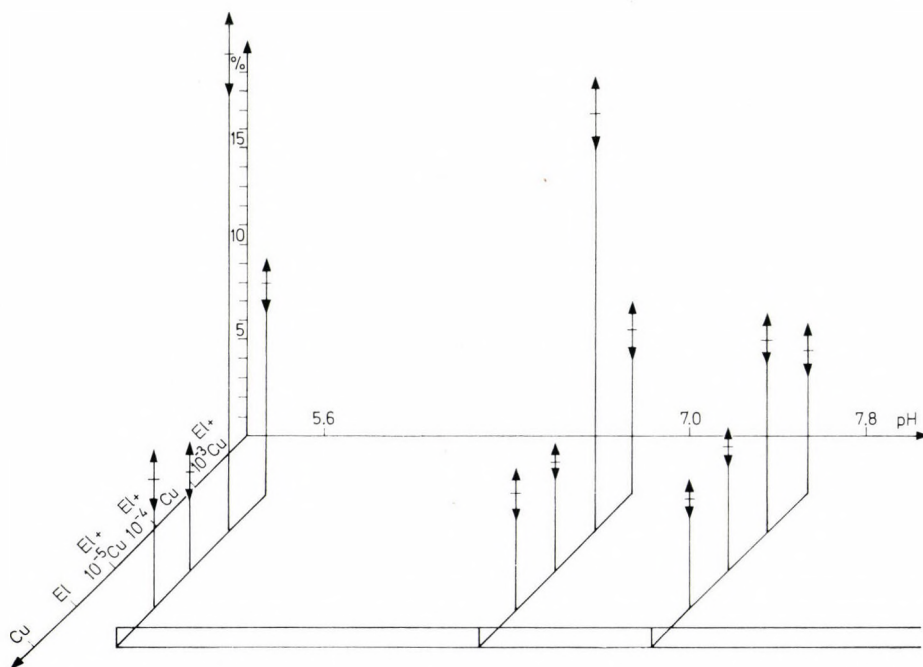



Fig. 1. Frequency of chromosome aberrations resulted by simultaneous EI and copper treatment and various pH values

Table 1

Frequency of chromosome aberrations in barley seeds after EI *and subsequent copper ion treatment at several concentration and* pH

Concentration (M)	Aberration, %								
	5.6 pH			7.0 pH			7.8 pH		
	meta-phase	aberra-tion	%	meta-phase	aberra-tion	%	meta-phase	aberra-tion	%
$EI+10^{-5}Cu$	567	38	6.70±0.99	453	25	5.51±1.07	610	36	5.90±0.95
$EI+10^{-4}Cu$	493	37	7.51±1.12	509	34	6.67±1.02	538	33	6.13±1.03
$EI+10^{-3}Cu$	621	31	4.99±0.87	601	37	6.15±0.97	492	26	5.28±1.00
$2.3\times10^{-3}EI$	423	27	6.38±1.18	385	23	5.97±1.20	562	32	5.69±0.97

much lower concentration than we used. It can be attributed with lower copper permeability of barley cell membrane. There can be thought on other causes, too, in connection with metabolism.

The ascertainment of the copper effect needs additional studies. EI treatment of barley seeds in the presence of copper ions results in more frequent occurrence of chromosome aberrations. Presumably Cu^{2+} can be an inhibitor of repair enzymes, and this is why it pollutes the environment and living organisms.

ACKNOWLEDGEMENTS

The author is grateful to Miss A. Fodor for her help during preparation of the manuscript.

REFERENCES

Bari, G. 1963: The mutagenic effect of ethyl-methanesulfonate alone and in combination with copper on wheat. *Caryologia* **16:** 619.

Grinich, L. I. 1981: Change of the mutagenic effectiveness in EMS-combined treatments on *Crepis capillaris.* (In Russian) In: Theory of chemical mutagenesis. Nauka.

Konzak, C. F., Nilan, R. A., Froese-Gertzen, E. E., Foster, R. F., Heiner, R. E. 1964: Experimental control over the action of chemical mutagens. *Techn. Meeting on Use of Induced Mutations in Plant Breeding,* IAEA-FAO, Rome.

Moutschen-Dahmen, J., Moutschen-Dahmen, M. 1963: Intéractions ioniques dans les effects radiomimétiqes du methane-sulfonate d'ethyl (EMS) sur les chromosomes de *Vicia faba. Rad. Bot.,* **3:** 297.

Nilan, R. A., Konzak, C. F., Heiner, R. E., Froese-Gertzen, E. E. 1964: Chemical mutagenesis in barley. Barley Genetics. 1 35–54 *Proc. Ist Intern. Barley Genet. Symp. Wageningen,* 1963. Pudoc, Wageningen.

Pusztai, T., Végh, A. 1978: Mutagenic effects of pesticides. 1. Cytological effects on some substituted urea herbicides in barley. *Acta Bot. Acad. Sci. Hung.* **24:** 327–342.

Acta Botanica Hungarica 33 (3—4), pp. 239—248 (1987)

DAMAGING EFFECT OF HORMONE-BASE HERBICIDE ON THE PETIOLE OF *ACER NEGUNDO* L.

F. Herdi

HUNGARIAN ACADEMY OF SCIENCES, RESEARCH INSTITUTE FOR PLANT PROTECTION, BUDAPEST, HUNGARY

(Received: 7, August 1984)

Dikotex 40 EC (MCPA) caused damage to *Acer negundo* leaves, manifest in external morphological features as well. The damage was due to the herbicide having been carried away by wind. The deleterious effect of the herbicide was evaluated by microscope examinations of sections prepared from the petiole. The thickness of the cuticle, and the wall thickness of hypoderma-, parenchyma- and schlerenchyma cells were measured. Changes of peripheric and median vascular bundles in the petiole were followed. The results of measuring were evaluated by double t-test.

The data obtained show that the cuticle on the epidermal surface of the damaged petiole is much thicker than the cuticle of the control petiole. The walls of hypoderma-, parenchyma- and schlerenchyma cells in the damaged petiole were thinner than in the control petiole. The greatest difference between damaged and control petiole was seen in the wall thickness of the schlerenchyma cells.

The vascular system is divided in an external peripheric- and an internal median region. The peripheric region consists of collateral closed bundles set in a circle, the median region is a large arched vascular bundle of collateral structure in the centre of the petiole. Under the influence of MCPA concentric vascular bundles of complicate structure developed at the outer side of the peripheric region, and the median vascular bundle broke up into smaller vascular bundles.

All in all, MCPA caused deformation of leaves and damage to tissue elements in the petiole.

Introduction

The hormone-base herbicides equally act on aboveground- and underground plant parts, and induce deformations in them (Ubrizsy et al. 1969). These herbicides cause damage and destruction mostly of dicotyledonous plants. The shoots show distortion, twisting, fasciation under the influence of these products. Leaves become funneliform (Buhl 1958, Ubrizsy 1962), entwined (Way 1962, 1963a, 1964, Kiermayer cit. Audus 1964); in grape-vine "fanleaf" and "ginkgo-leaf" symptoms (Ubrizsy 1962, Szatala 1967) can be observed. Other changes in shape and deformations were found by Andersen, Bachthaller, Hanf cit. Ubrizsy (1962), Ubrizsy *et al.* (1969), Terpó *et al.* (1971), Way (1963, 1963b, 1964a). Distortion and necrosis occurred with the fruit (Ubrizsy 1962) and root (Arlt et al. 1973, Buhl 1958, Lehoczky 1979, Way 1962, 1963a, 1964) as well.

Considerable damages are caused by the hormone-base herbicides at the time of cell differentiation (Watson 1948). Great influence is exercised by these products on cell-wall formation too (Gorter, Gifford cit. Audus 1964, Herdi 1981, 1981a, 1982, 1982a, 1983, 1983a). To 2,4-D cambium, endodermis, embryonal pericycle and phloem gave the most remarkable response (Swanson cit. Klingman 1963, Beal cit. Audus 1964). Dichlobenil and dicamba

Actual adress: Meriklon GT, Budapest, P.O. Box 86 H-1525

damaged the phloem, the cambium and the adjacent parenchyma (PATE *et al.* 1965). MEYER (1970) observed damages in the xylem and phloem of stem and root in response to picloram and 2,4,5-T. EAMES (1949) gave account of abnormal development, elongation of vascular bundles in leaves. BRADLEY *et al.* cit. AUDUS (1976) found the diameter of the petiole to have grown. HERDI (1979, 1981, 1983, 1983a) reported deformation and multiplication of vascular bundles under the influence of 2,4-D, MCPA and dicamba. SOROKIN *et al.* (1965) observed IAA induced hyperplasia and deficient xylem formation in bean shoots.

Materials and methods

Damage caused by Dikotex 40 EC (32% MCPA) in the tissue structure of the petiole of *Acer negundo* was studied. The *Acer negundo* tree was 25 m off the adge of a spring barley field sprayed with DIKOTEX 40 EC (3.5 litre/ha), and suffered damage from the herbicide carried away by the wind. The symptoms were observed on the leaves at the end of May. At the beginning of July a shoot with 12 leaves was collected from the damaged tree and a 5-leaf shoot from an intact tree. The leaves were fixed in 40% alcohol for the purpose of preparing sections of the petiole. Sample required for the sections was taken from the middle of the petiole of each leaf on the shoot.

The sections were made with an MC-2 type slide-microtom supplied with a KTOC-2 electric freezing appliance. For staining safranine and EHRLICH's acid haematoxylin were used.

With the evaluation of the experiment in view the thickness of cuticle and the wall thickness of hypoderma-, parenchyma- and schlerenchyma cells were measured, and the MCPA induced changes in the vascular system followed.

The data of measuring were evaluated by double t-test; the results are contained in Table 1.

Results

The foliage leaves of *Acer negundo* are imparipinnate, bifacial, with 3–5 leaflets.

The *control plant* had healthy, intact leaves; the 1st to 3rd leaf on the shoot consisted of three (Fig. 1), the 4th and 5th leaf of five leaflets (Fig. 2).

The *damaged plant* showed signs of external damage on most of the leaves (crisped margin, oblong shape, intervenial scoops). The 3rd and 4th leaf on the shoot (Fig. 3) consisted of three leaflets, the 5th and 6th (Fig. 3), further the 7th and 9th leaf (Fig. 4) were composed of five leaflets, the 10th and 12th leaf (Fig. 5) had seven leaflets. In the 8th (Fig. 4) and 11th leaf (Fig. 5) the uppermost leaflet and the one immediately below were grown together, so that the 8th leaf consisted of six instead of seven leaflets (Fig. 4), and the 11th leaf had four instead of five leaflets (Fig. 5).

The cross section of the petiole of *Acer negundo* is circular. The surface of epidermis on the petioles of both the control and damaged leaves is covered by a thick cuticle which, however, is much thicker in the case of damaged leaves (4.44 μm) than in the control (3.72 μm) (Figs 6–10), Table 1. The cuticle is thickest on the petioles of those leaves (5th to 8th leaf) which show the most serious exterior damages.

Under the epidermis the 4–6-cell thick hypoderm is found. The hypoderm is characterized by uniformly thickened cell-walls. In the petiole of each damaged leaf the walls of the hypoderm cells (Figs 6–10) are thinner than those of the control cells (Table 1). They are thinnest (0.97 μm) in the case of the 3rd damaged leaf, show some thickening (1.07 μm) with the 5th to 8th damaged leaves, and are nearly as thick (1.31 μm) as those in the control (1.37 μm) with the 9th to 12th damaged leaves.

Beneath the hypoderm lies the parenchyma (Figs 6–10) which consists of larger cells with thin (Table 1) pitted walls. The walls of the parenchyma cells in the petiole of the 3rd

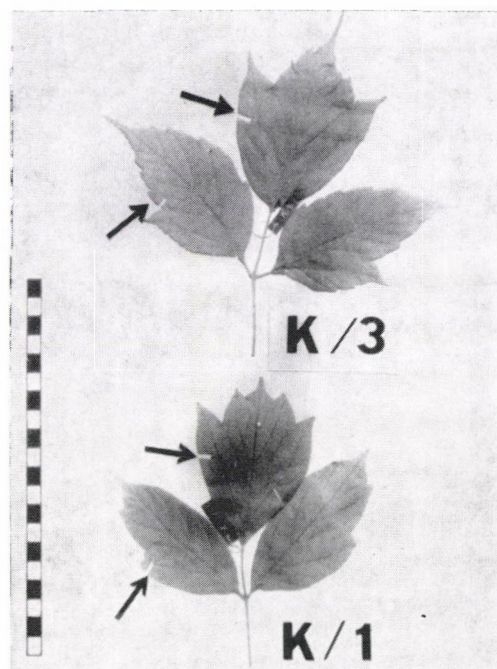



Fig. 1. 1st and 3rd leaf on the shoot of the control plant (the arrows indicate the places of samples excised from the leaf-blade to prepare sections from)

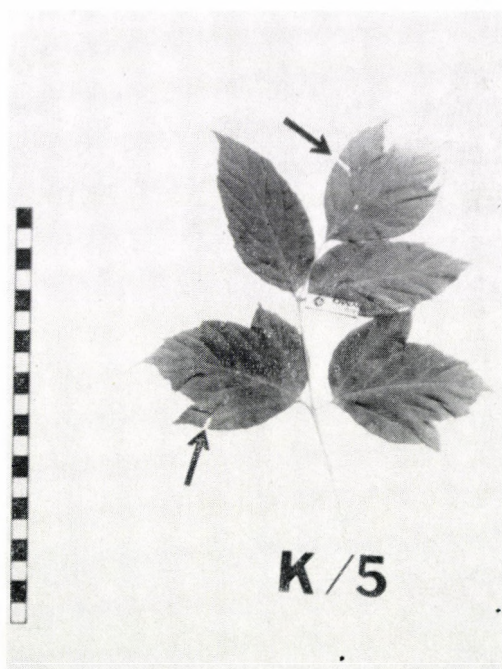



Fig. 2. 5th leaf on the shoot of the control plant (the arrows indicate the places of samples excised from the leaf-blade to prepare sections from)

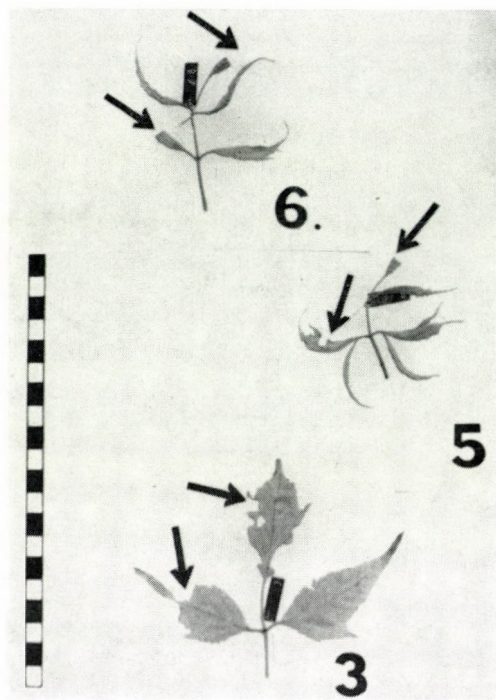



Fig. 3. 3rd, 5th and 6th leaf on the shoot of the damaged plant (the arrows indicate the places of samples excised from the leaf-blade to prepare sections from)

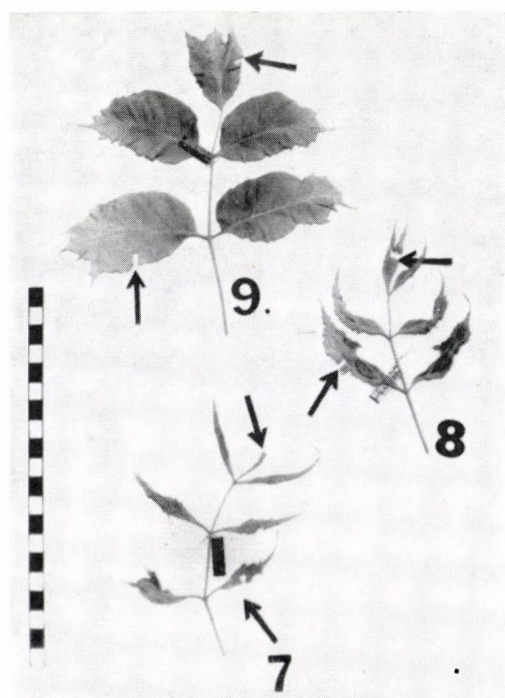



Fig. 4. 7th, 8th and 9th leaf on the shoot of the damaged plant (the arrows indicate the places of samples excised from the leaf-blade to prepare sections from)

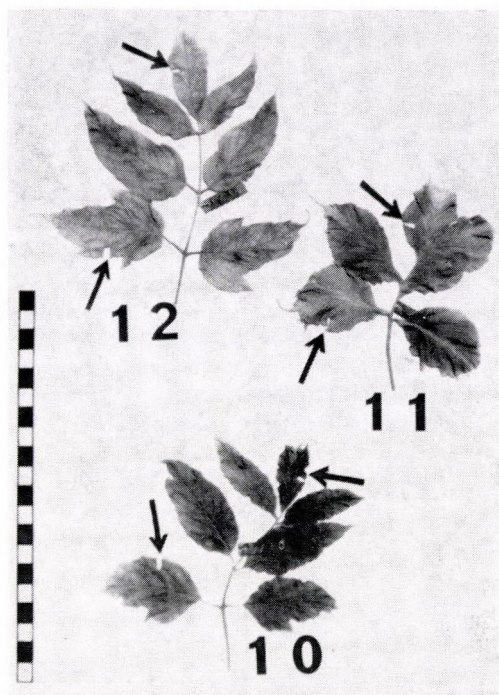



Fig. 5. 10th, 11th and 12th leaf on the shoot of the damaged plant (the arrows indicate the places of samples excised from the leaf-blade to prepare sections from)

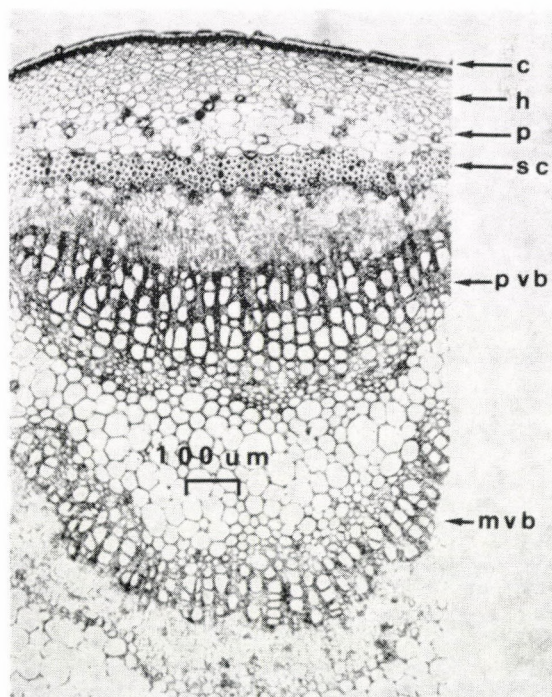



Fig. 6. Detail of cross section from the petiole of the 5th control leaf (c = cuticle, h = hypoderm, p = parenchyma, sc = sclerenchyma, pvb = peripheric vascular bundle, mvb = median vascular bundle)

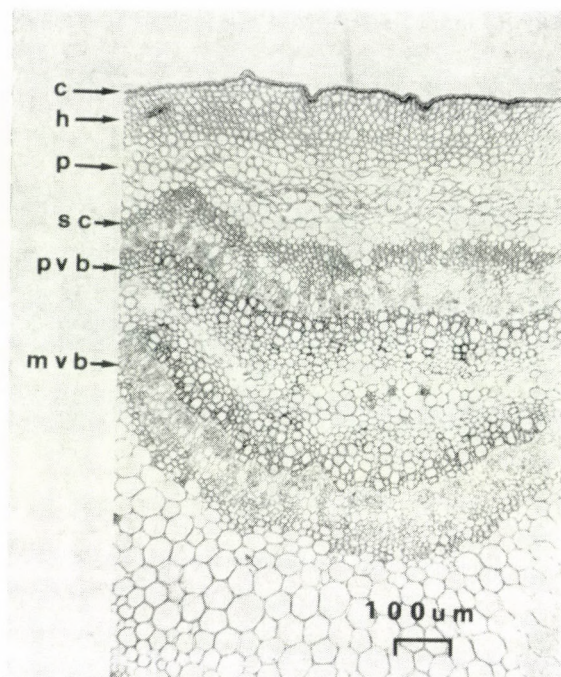



Fig. 7. Detail of cross section from the petiole of the 3rd damaged leaf (c = cuticle, h = hypoderm, p = parenchyma, sc = sclerenchyma, pvb = peripheric vascular bundle, mvb = median vascular bundle)

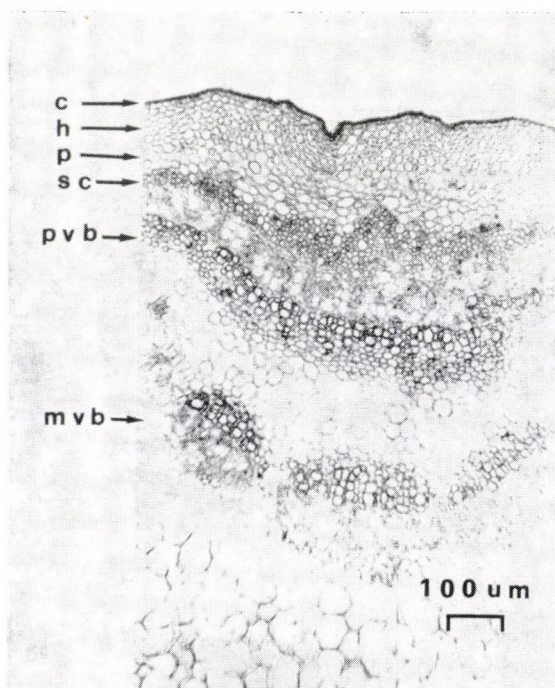



Fig. 8. Detail of cross section from the petiole of the 7th damaged leaf (c = cuticle, h = hypoderm, p = parenchyma, sc = sclerenchyma, pvb = peripheric vascular bundle, mvb = median vascular bundle)

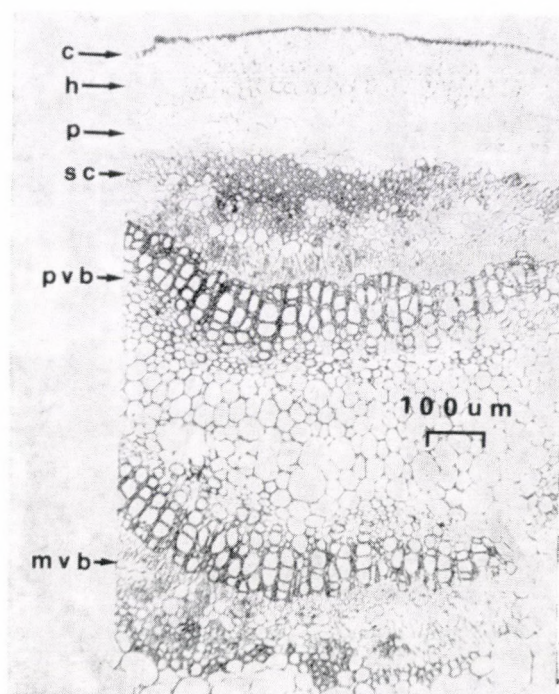



Fig. 9. Detail of cross section from the petiole of the 9th damaged leaf (c = cuticle, h = hypoderm, p = parenchyma, sc = sclerenchyma, pvb = peripheric vascular bundle, mvb = median vascular bundle)

damaged leaf are thinner (0.80 μm) than those in the control (0.93 μm). They are thinnest in the petioles of the 5th to 8th leaves (0.66 μm). In the petioles of the 9th to 12th leaves the parenchyma cell-walls sho w some thickening compared to those in the petioles of the 5th–8th

Table 1

Changes in the thickness of cuticle and wall thickness of hypoderm-, parenchyma- and sclerenchyma cells in the petiole of Acer negundo under the influence of MCPA

Treatment	Thickness of cuticle μm	Hypoderm cells μm	Wall thickness of parenchyma cells μm	Sclerenchyma cells μm
C*	3.72±0.63	1.37±0.25	0.93±0.16	2.54±0.48
1**	+4.22±0.52	0.97±0.17	0.80±0.06	1.36±0.17
2***	4.60±0.45	1.07±0.21	0.66±0.08	0.70±0.17
3****	4.52±0.45	++1.31±0.20	0.81±0.11	1.40±0.15

+ = $p < 1\%$
++ = non-significant, in the other cases compared to the control $p < 0.1\%$
* = average of measuring data for the 1st, 3rd and 5th control leaves
** = average of measuring data for the 3rd damaged leaf
*** = average of measuring data for the 5th, 6th, 7th and 8th damaged leaf
**** = average of measuring data for the 9th, 10th, 11th and 12th damaged leaf

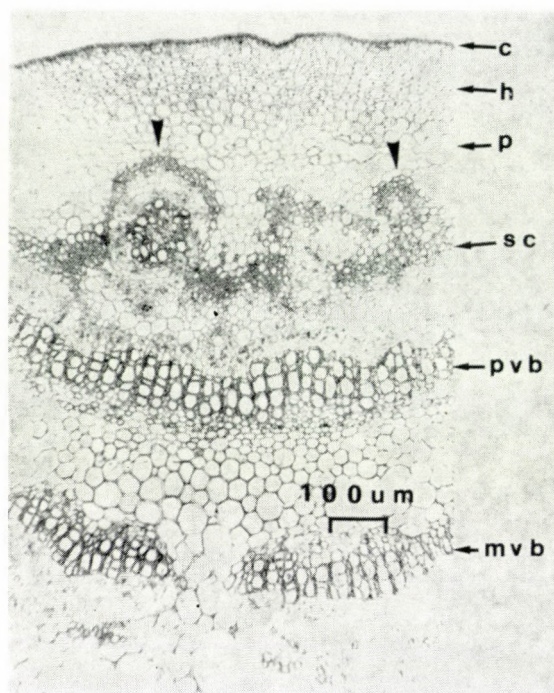



Fig. 10. Detail of cross section from the petiole of the 11th damaged leaf (c = cuticle, h = hypoderm, p = parenchyma, sc = sclerenchyma, pvb = peripheric vascular bundle, mvb = median vascular bundle). On the outer side of the peripheric conducting tissue system concentric bundles of somevhat complicate structure (indicated by arrows) are seen. The nedian vascular bundle is broken up into parts

leaves, they are about as thick (0.81 μm) as those in the petiole of the 3rd damaged leaf.

The next tissue layer under the cortical parenchyma is the sclerenchyma ring formed of the phloem of vascular bundles (Figs 6–10). The width of the sclerenchyma ring is not uniform, ranging between 26.40 μm and 41.83 μm in the control petiole. The valls of the sclerenchyma cells are very thick (2.54 μm, Table 1). The sclerenchyma ring in the petiole of the damaged 3rd leaf — just as in the control petiole — is not uniformly wide, and is narrower compared to the control (18.60 μm–41.83 μm). The sclerenchyma cell-walls are substantially thinner (1.36 μm) than in the control (Table 1).

The sclerenchyma ring in the petiole of the damaged 5–8th leaf is much narrower than in the control petiole (18.87 μm–33.72 μm), and is again of varying width. The cell-walls are very thin compared to the control, the thinnest of all in the petioles of these leaves (0.70 μm, Table 1).

The sclerenchyma ring in the petioles of the damaged 10th–12th leaves is not uniformly wide either, and is remarkably narrower (19.41 μm–34.08 μm) than in the control petioles. The sclerenchyma cell-walls are essentially thinner (1.40 μm) compared to the control, though thicker than in the petioles of th 5th–8th leaves (Table 1).

The conducting tissue system is divided in a peripheric- and a median region. The peripheric region is formed by collateral bundles set close to one another in a circle; in the course of the petioles thickening they interlock and give then the semblance of a continuous

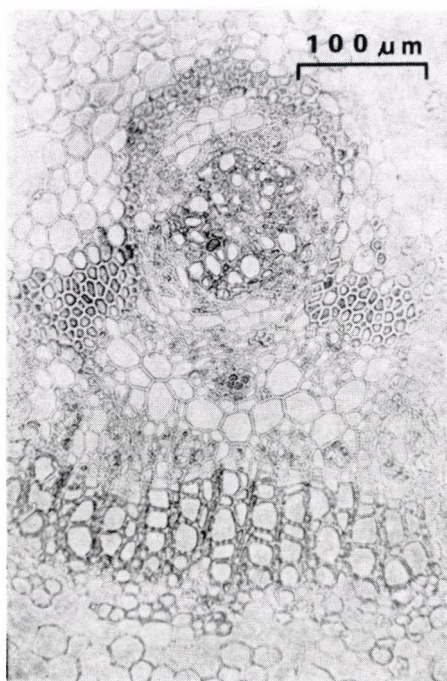



Fig. 11. Concentric vascular bundle in the petiole of the 11th damaged leaf

conducting tissue system. In the centre of the petiole a large arched, so-called median vascular bundle of collateral structure is found.

In the petioles of control- and damaged leaves the collateral closed bundles set in a circle to form the peripheric region (Figs 6–10) are found close to one another. While the petiole thickens these bundles interlock and form a continuous conducting tissue system. In the petiole of the damaged 5th leaf these bundles mostly are apart. In the petioles of the damaged 8th, 10th and 11th leaf concentric bundles of somewhat complicated structure are found on the outer side of this vascular system (Figs 10 and 11). In the petioles of all control leaves and in those of the 3rd, 4th and 6th leaf of the damaged plant there is a large, arched median vascular bundle in the centre (Figs 6 and 7). In the petioles of the 5th and 7th–12th leaves of the damaged plant the median vascular bundle is brooken up into smaller vascular bundles (Figs 8–10).

As a conclusion it can be established that in consequence of the MCPA-containing Dikotex 40 EC herbicide having been carried away by wind, the leaves of *Acer negundo* suffered considerable morphological changes. In the inner structure of the petiole the deleterious effect of MCPA was evident: the cell-walls became thicker, changes occurred in the vascular system, the median vascular bundle broke up into smaller bundles, and on the outer side of the peripheric region concentric vascular bundles of somewhat complicated structure developed.

ACKNOWLEDGEMENTS

The author is indebted to Dr. L. FRIDVALSZKY, scientific consultant at the Department for Plant Organization, Loránd Eötvös University, for his assistance in evaluating the microscope sections, and for his help concerning the subject in general; and thanks are due to Mrs. S. ZALINSZKY for her work in processing the sections.

REFERENCES

Herdi, F. 1981: Szöveti elváltozások dicamba hatására a napraforgó (*Helianthus annuus* L.) lomblevelében (Dicamba induced changes in the tissues of sunflower (*Halianthus annuus* L.) foliage leaves). — *Növénytermelés*, **30:** 229–239.

Herdi, F. 1981a: A napraforgó (*Helianthus annuus* L.) levélnyelében levő szállítónyalábok szöveti elváltozása 2,4-D hatására (2,4-D induced changes in the tissues of vascular bundles in the petiole of sunflower (*Helianthus annuus* L.) (*Növényvédelem*), **17:** 176–186.

Herdi, F. 1982: MCPA hatása a napraforgó (*Helianthus annuus* L.) levélnyelében lévő szállítónyalábokra (Effect of MCPA on the vascular bundles in the petiole of sunflower (*Helianthus annuus* L.)), *Növényvédelem* **18:** 53–62.

Herdi, F. 1982a: Dicamba hatása a napraforgó (*Helianthus annuus* L.) levélnyelében lévő szállítónyalábokra (Effect of dicamba on vascular bundles in the petiole of sunflower (*Helianthus annuus* L.). — *Növényvédelem*, **18:** 302–312.

Lehoczky, J. 1979: Veszélyes jelenség a 2, 4, 5-T által indukált léggyökérképződés a szőlőtőkéken (A dangerous phenomenon: 2, 4, 5-T induced air root formation in grape-vine). — *Szőlőtermesztés*, **1:** 11–15.

Szatala, Ö. 1967: Hormonos gyomirtószerek okozta károsodások (Damages caused by hormone-containing herbicides). — *Kertészet és Szőlészet*, **16** (8), 28–29.

Terpó-Pomogyi, M., Terpó, A. 1971: Dikonirt (2, 4-D) hatása a *Vitis vinifera* L. morfogenetikai és anatómiai tulajdonságaira (Effect of Dikonirt (2, 4-D) on the morphogenetic and anatomical features of *Vitis vinifera* L.). — *Szőlő- és Gyümölcstermesztés*, **6**, 221–241.

Ubrizsy, G. 1962: *Vegyszeres Gyomirtás* (Chemical weed control). — Mezőgazdasági Kiadó, Budapest

Ubrizsy, G., Gimesi, A. 1969: *A Vegyszeres Gyomirtás Gyakorlata* (Practice of chemical weed control). — Mezőgazdasági Kiadó. Budapest

Acta Botanica Hungarica 33 (3—4), pp. 249—278 (1987)

A PHYTOGEOGRAPHIC REVIEW OF TORTULA HEDW. SECT. RURALES DE NOT. (POTTIACEAE, MUSCI) IN HUNGARY

Z. Tóth

DEPARTMENT OF PLANT TAXONOMY AND ECOLOGY, L. EÖTVÖS UNIVERSITY, BUDAPEST, HUNGARY

(Received: 15, October 1986)

Distribution of the 13 Hungarian taxa of *Tortula* sect. *Rurales* based on herbarium studies, accompanied by detailed maps. Remarks on general distribution, based on herbarium and literature studies.

Introduction

The section *Rurales* of genus *Tortula*, especially the *Tortula ruralis* aggregate of this section, includes some of the most abundant mosses of the steppe and forest-steppe vegetation in Hungary and therefore plays a significant role in the water balance, nutrient cycling and humus formation of these communities. In dry grasslands (e.g. *Festucetum vaginatae*) the phytomass of mosses and lichens may exceed significantly that of the flowering plants (Simon and Kovács-Láng, 1976). As their abundance suggests, the moss tufts, composed mainly of the members of the *Tortula ruralis* aggregate, are important constituents of the productive layer in the ecosystem of nutrient poor sandy soils. The high abundance and considerable cover of Tortula species have been reported from many phytogeographical, phytosociological and ecological studies (Borbás, 1886; Győrffy, 1943; Zsolt, 1943; Soó, 1956; Boros, 1968; Simon and Kovács-Láng, 1972; Simon and Szerényi, 1975).

Material and methods

About 1250 herbarium specimens deposited in three herbaria in Hungary (BP, EGR, VBI) were analysed from floristic, taxonomic and biogeographic points of view. All specimens originale from the Carpathian Basin. Additional specimens collected by the author in Central Asia (Uzbekistan, USSR) were also used as comparative material.
The specimens were identified following W. Kramer's key (1980).
For mapping ground map and settlement list complied by Borhidi *et al.* (1968) were used.

Results

Thirteen taxa were identified in the material, they are:

— **T. calcicolens** W. Kramer
— **T. caninervis** (Mitt.) Broth. ssp. **spuria** (Amann) W. Kramer var. **spuria** nom. nov. (ICBN Art 26. 1). Syn: *T. caninervis* (Mitt.) Broth. ssp. *spuria* (Amann) W. Kramer var. *gypsophila* (Roth) W. Kramer
— **T. fragilis** Tayl.

— **T. intermedia** (Brid.) De Not. var. **intermedia**
— **T. intermedia** (Brid.) De Not. var. **calva** (Dur. et Sag.) Wijk et Marg.
— **T. latifolia** Bruch ex Hartm.
— **T. norvegica** (Web.) Lindb. var. norvegica
— **T. princeps** De Not.
— **T. ruralis** (Hedw.) Gaertn. et al. ssp. **hirsuta** (Vent.) W. Kramer var. **hirsuta**
— **T. ruralis** (Hedw.) Gaertn. et al. ssp. **hirsuta** (Vent.) W. Kramer var. **submamillosa** W. Kramer
— **T. ruralis** (Hedw.) Gaertn. et al. ssp. **ruralis** var. **ruralis**
— **T. ruraliformis** (Besch.) Ingh. var. **ruraliformis**
— **T. virescens** (De Not.) De Not. ssp. **virescens** var. **virescens**

Four of these taxa, *T. caninervis*, *T. norvegica*, *T. ruralis* ssp. *hirsuta* var. *hirsuta* and *T. ruralis* ssp. *hirsuta* var. *submamillosa* proved to be new to the Hungarian flora.

Phytogeographic overview

The maps showing the distribution of *Tortula* taxa in Hungary (Figs 14—21) were all prepared using the identified specimens. The other distribution maps (Figs 1—13) summarize data derived from the literature. Localities impossible to locate in geographic maps were excluded from the study.

Tortula calcicolens is distributed from the circumboreal to the warm-temperate zones. *Tortula caninervis* ssp. *spuria* var. *spuria* has a typical Turanian geographic range, it is a semi-desert species. In the Hungarian Plain it has an isolated, disjunct distribution, like some higher plants (e.g. *Kochia prostrata*). In the Moravian basin and the Rhône Valley in Valais this species occurs as a relict. *Tortula fragilis* is distributed in the warm-temperature and tropical zones, and does not occur in Hungary. *Tortula intermedia* var. *intermedia* is considered as an Atlantic–Mediterranean flora element with disjunct occurrences in California and British Columbia. *Tortula intermedia* var. *calva* is a Central European–submediterranean taxon. The distribution of *Tortula latifolia*, *T. norvegica* and *T. ruralis* ssp. *hirsuta* var. *hirsuta* is circumboreal, although *T. norvegica* has alpin character, *T. latifolia* is a flora element of the temperate while *T. ruralis* ssp. *hirsuta* var. *hirsuta* of the warm-temperate zone. *Tortula princeps* and *T. ruralis* ssp. *ruralis* var. *ruralis* are of a bipolar distribution. *T. princeps* occurs in the warm-temperate and subtropical zones and wider distributed than *T. ruralis* ssp. *ruralis* var. *ruralis*, which is confined to the temperate zone. *Tortula ruraliformis* var. *ruraliformis* is found in the warm-temperate zone, whereas *Tortula virescens* ssp. *virescens* var. *virescens* is an Atlantic–Mediterranean flora element. The taxonomic status and delimitation of *Tortula ruralis* ssp. *hirsuta* var. *submamillosa* is not yet clarified exactly and therefore its phytogeography is to be studied later.

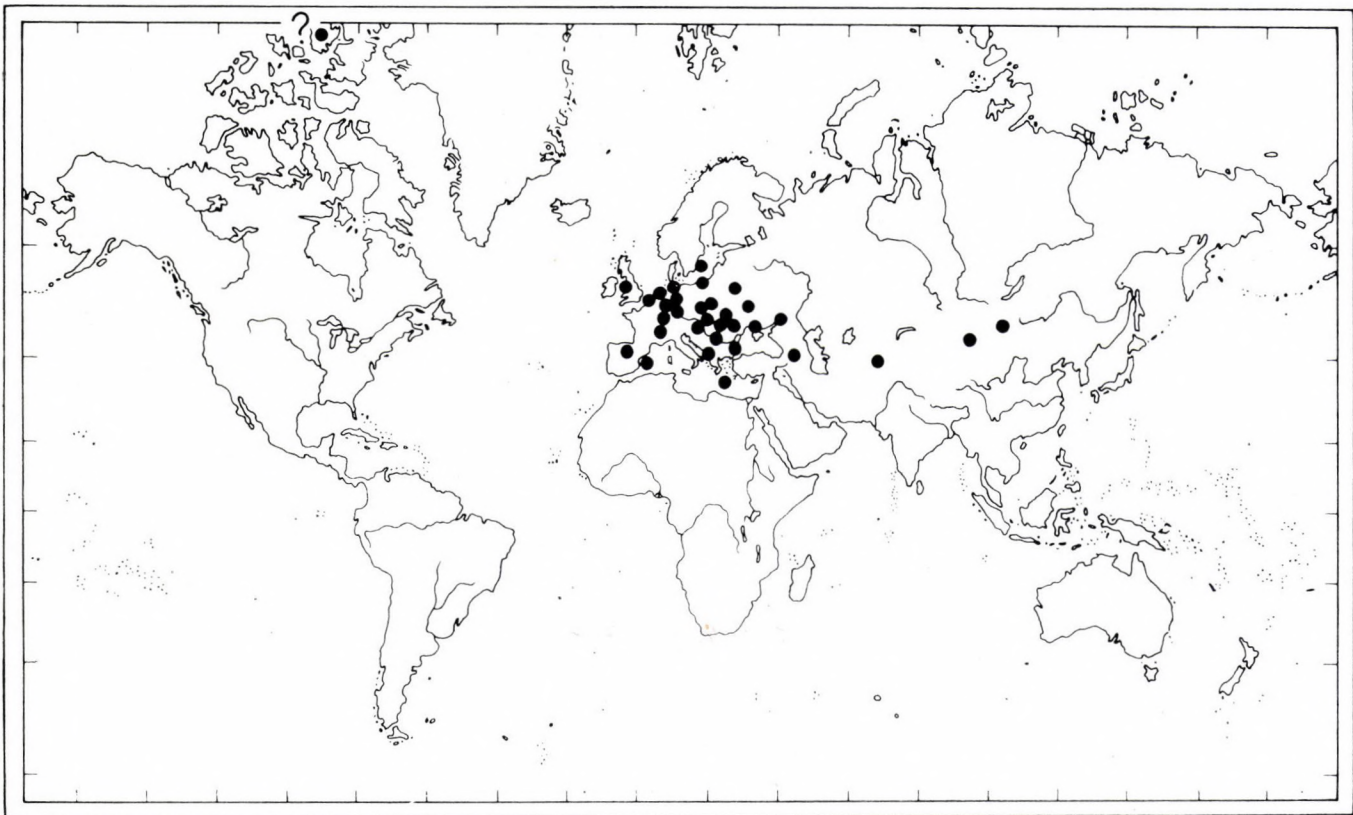



Fig. 1. The distribution of *T. calcicolens* in the world

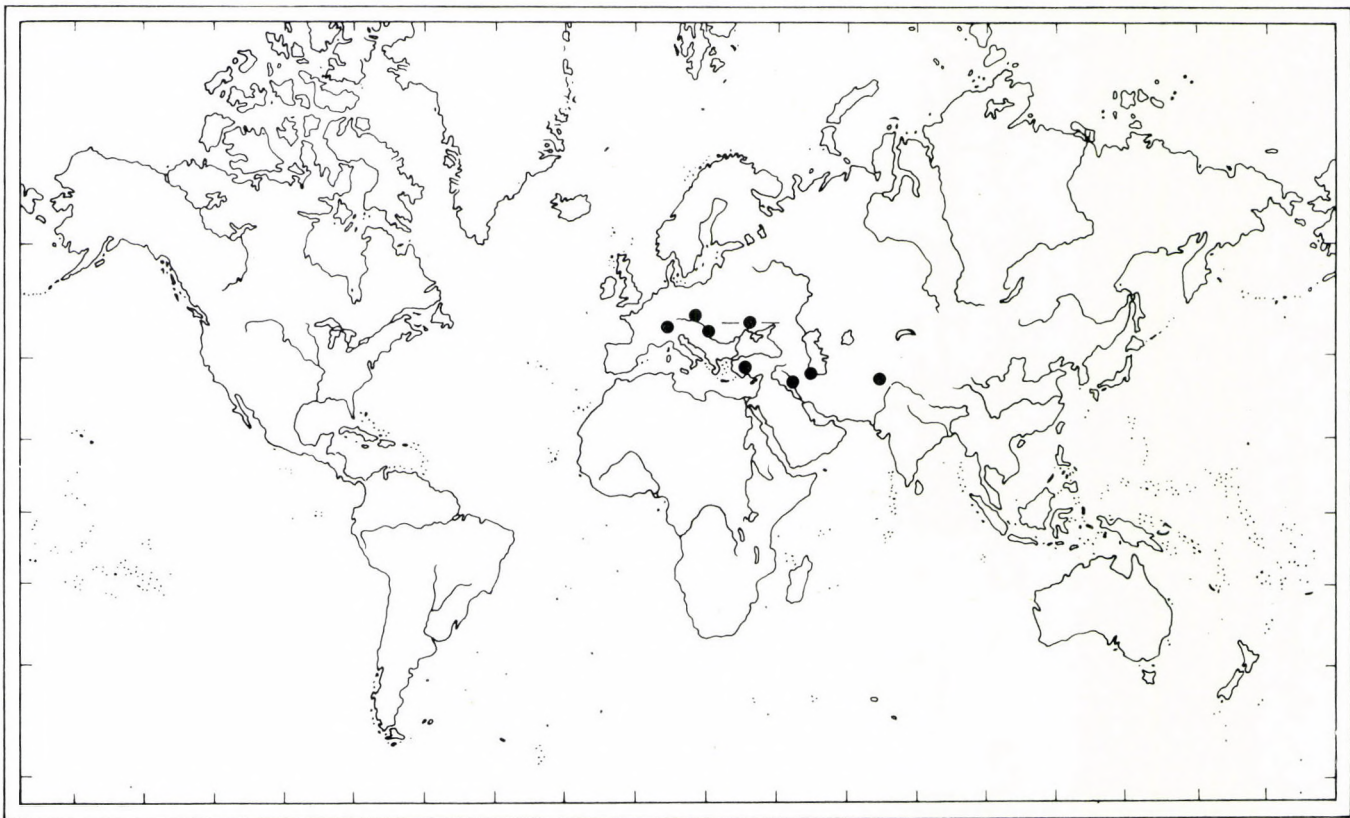



Fig. 2. The distribution of *T. caninervis* ssp. *spuria* var. *spuria* in the world

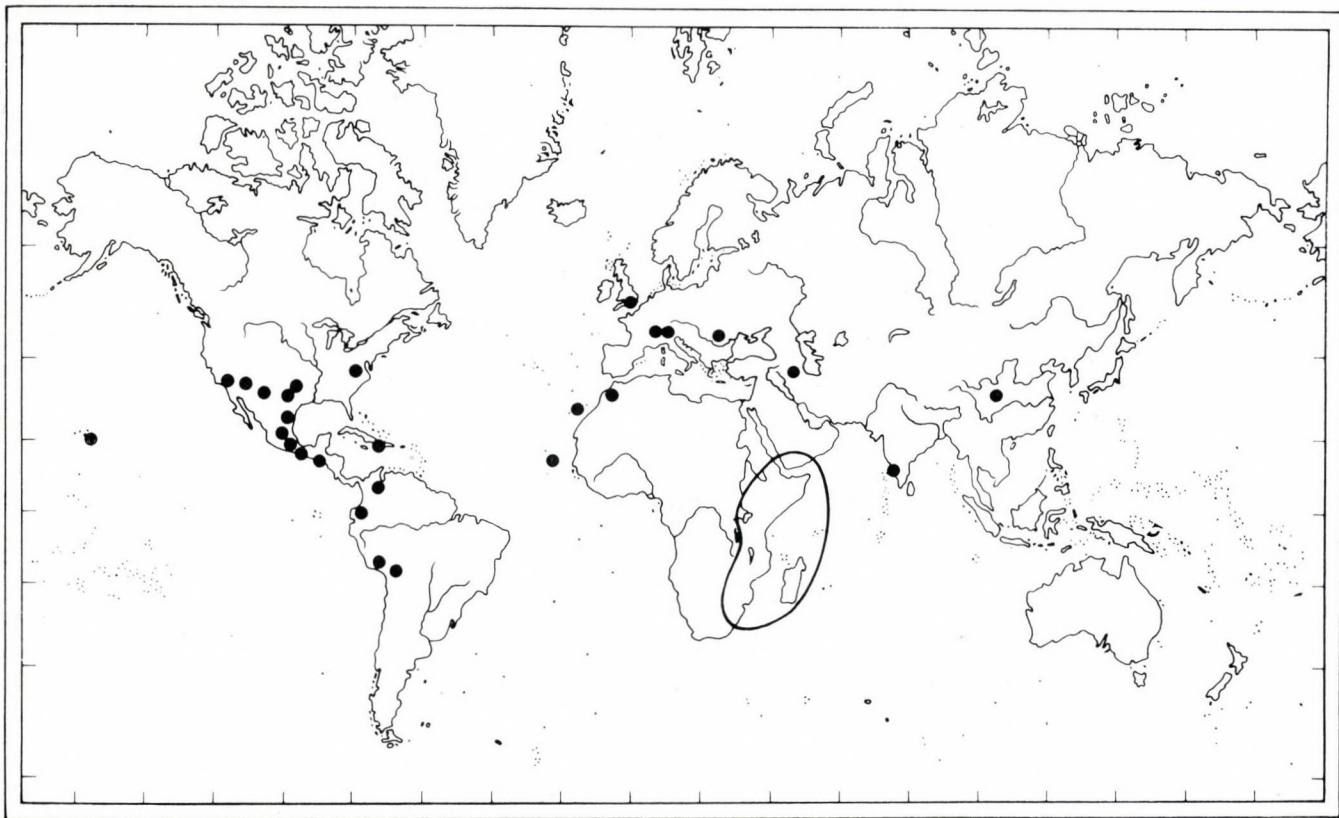



Fig. 3. The distribution of *T. fragilis* in the world (this taxon is very common in the area outlined)

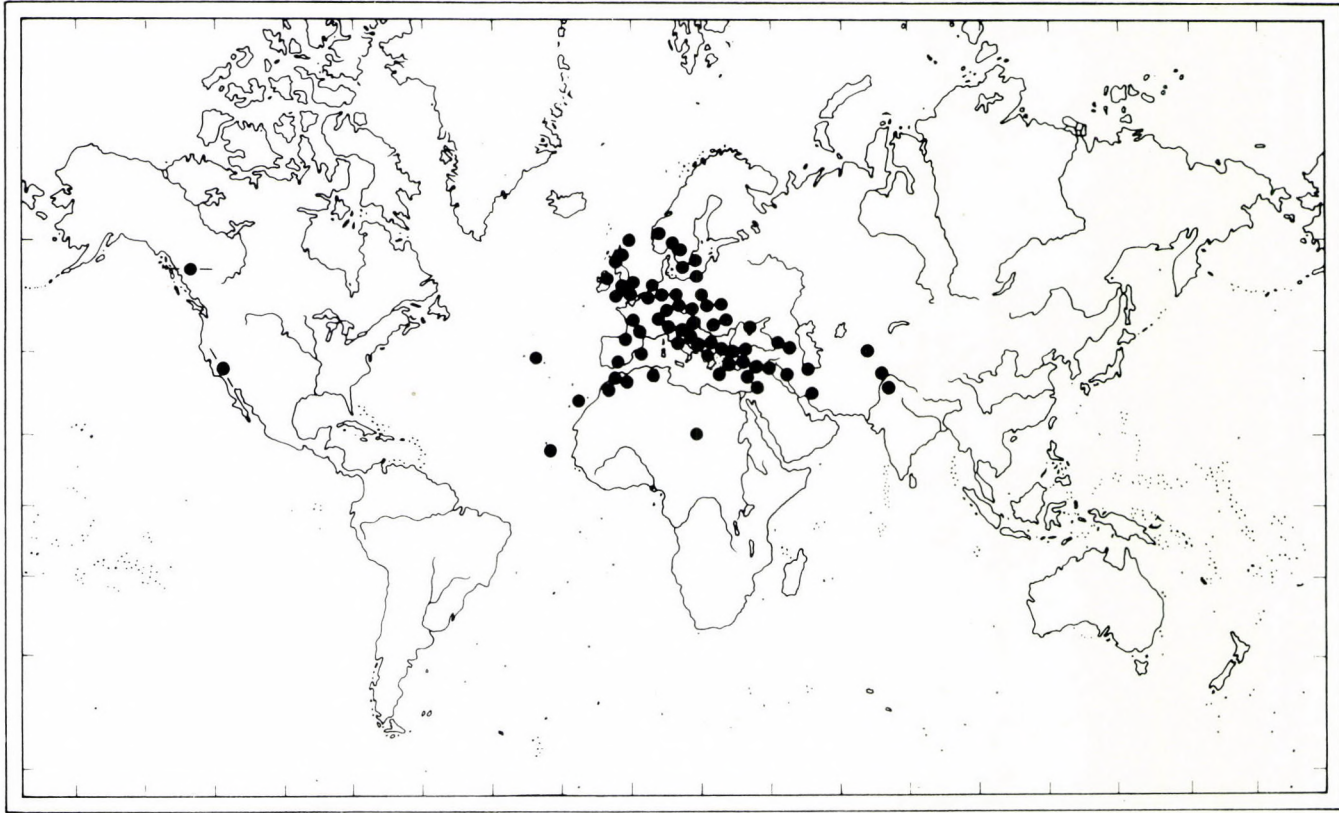



Fig. 4. The distribution of *T. intermedia* var. *intermedia* in the world

Fig. 5. The distribution of *T. intermedia* var. *calva* in the world

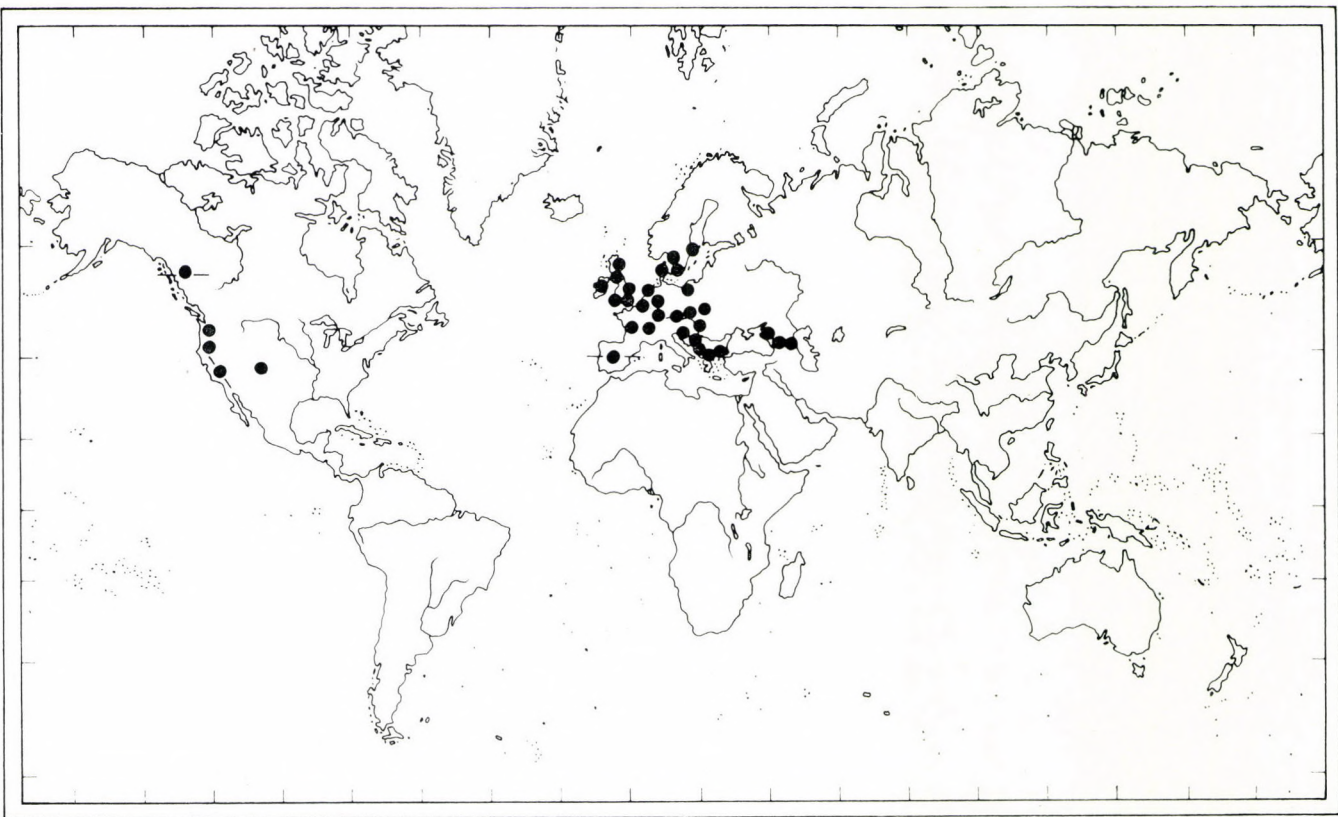



Fig. 6. The distribution of *T. latifolia* in the world

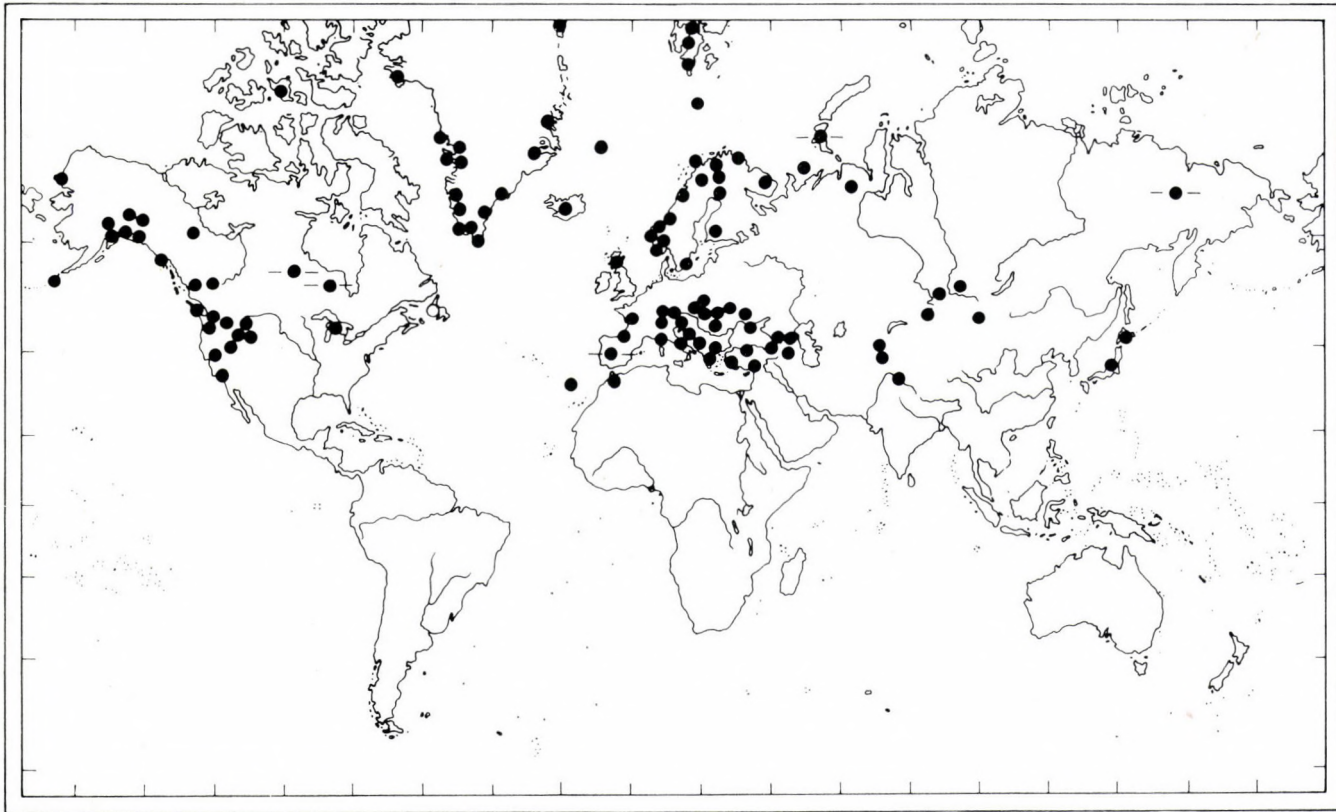



Fig. 7. The distribution of *T. norvegica* in the world

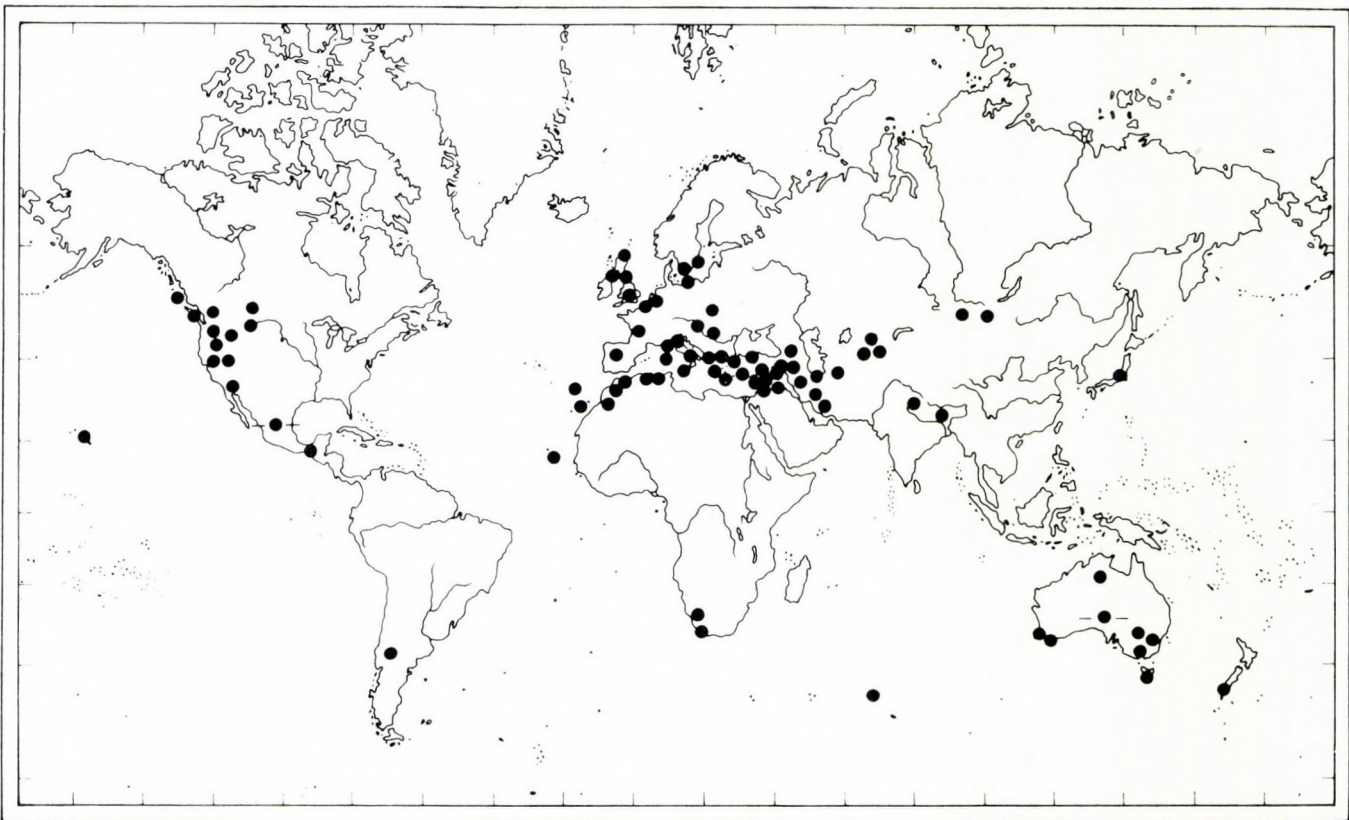



Fig. 8. The distribution of *T. princeps* in the world

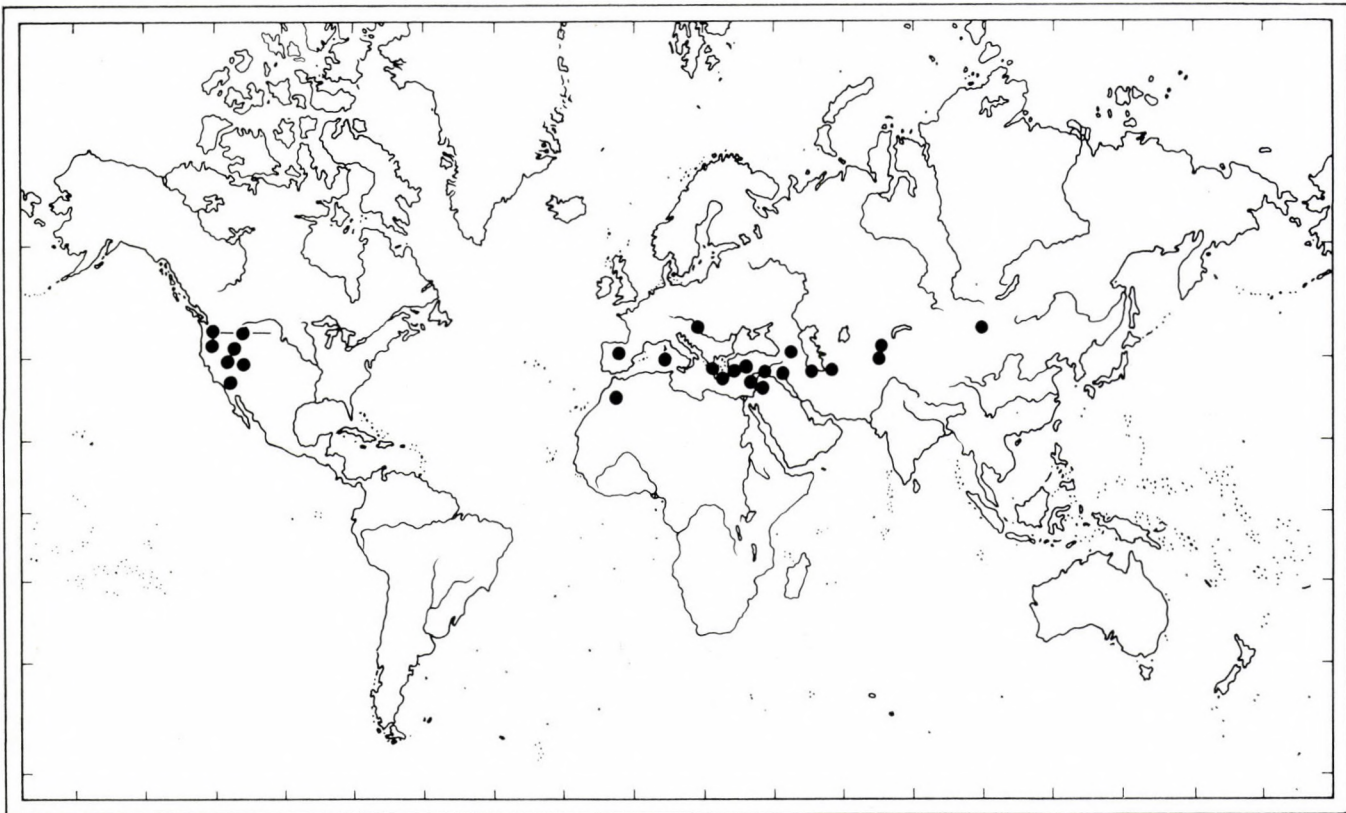



Fig. 9. The distribution of *T. ruralis* ssp. *hirsuta* var. *hirsuta* in the world

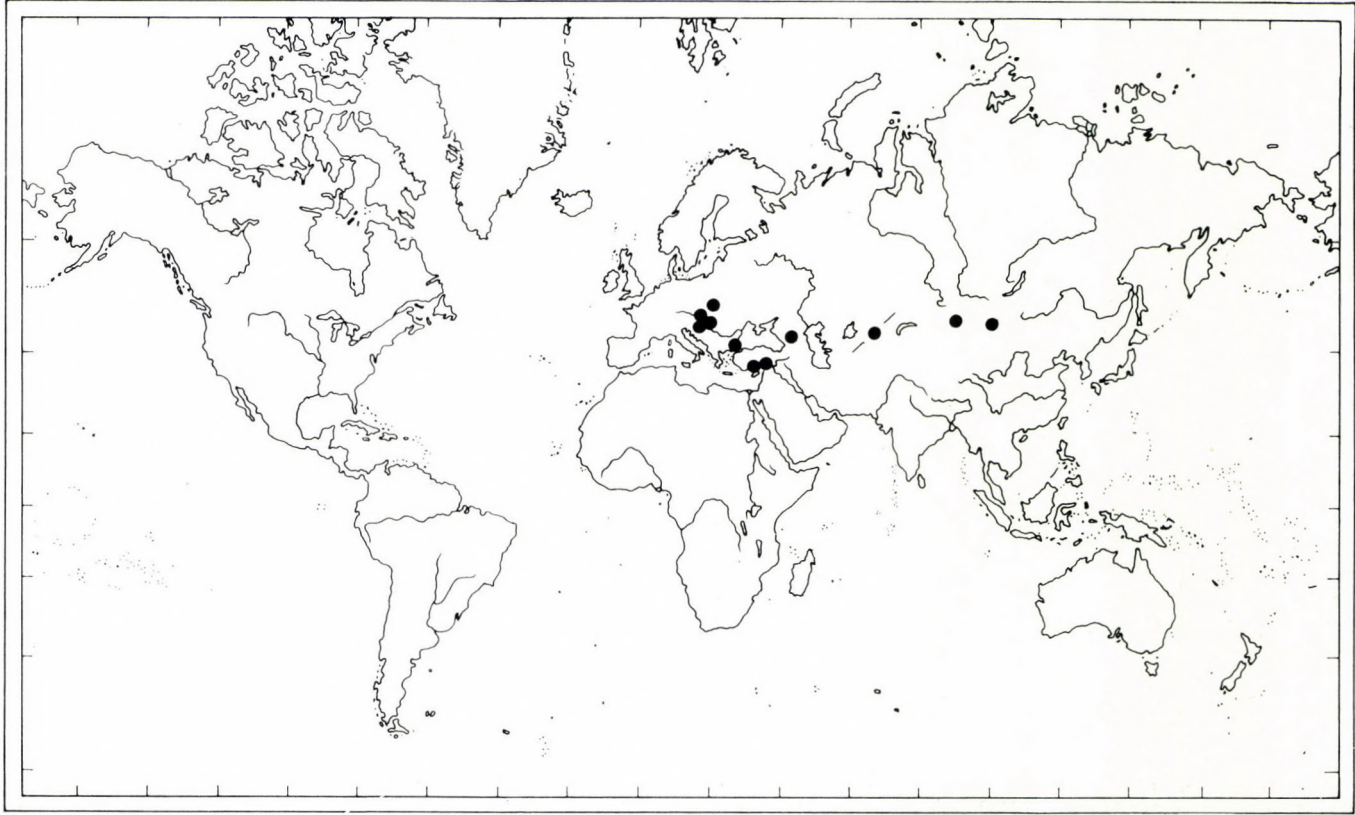



Fig. 10. The distribution of *T. ruralis* ssp. *hirsuta* var. *submamillosa* in the world

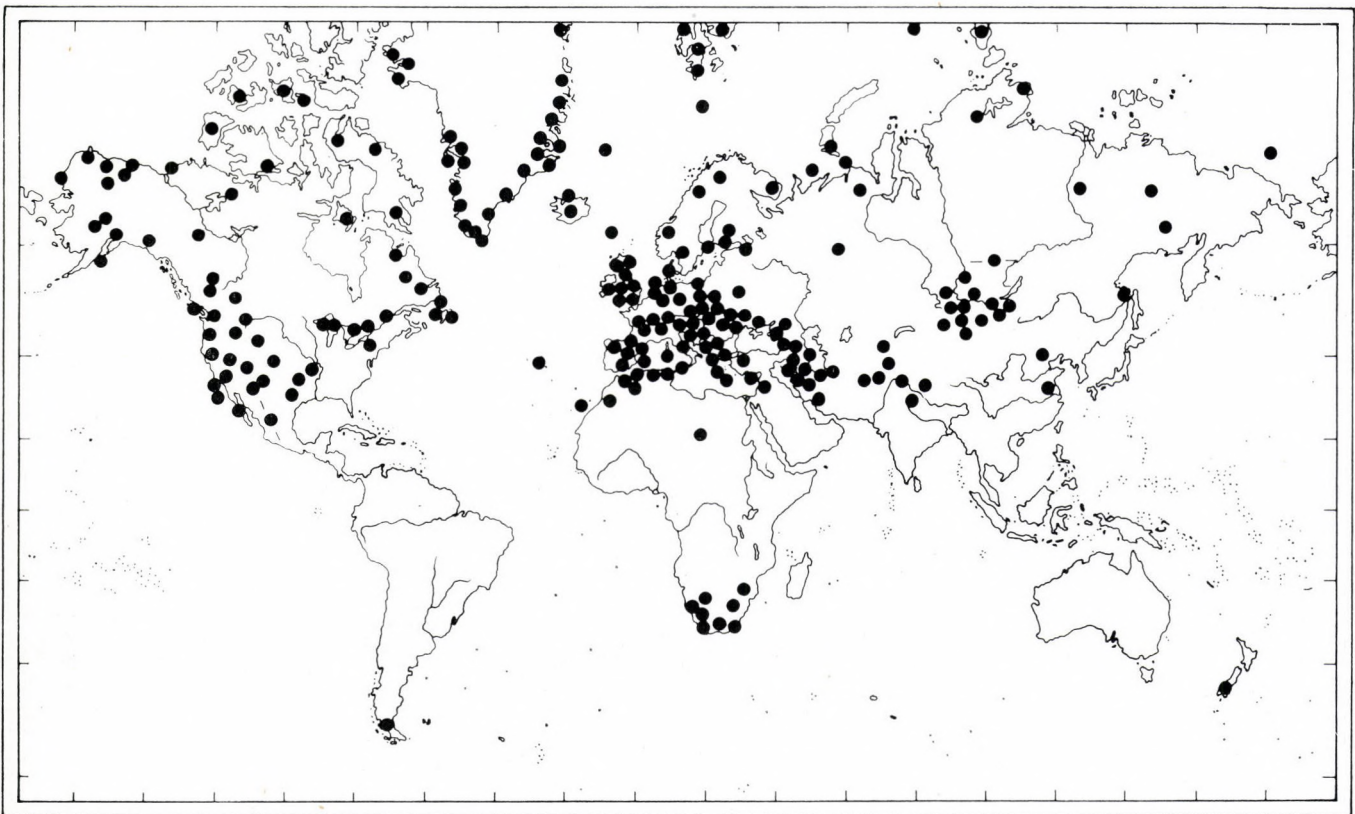



Fig. 11. The distribution of *T. ruralis* ssp. *ruralis* var. *ruralis* in the world

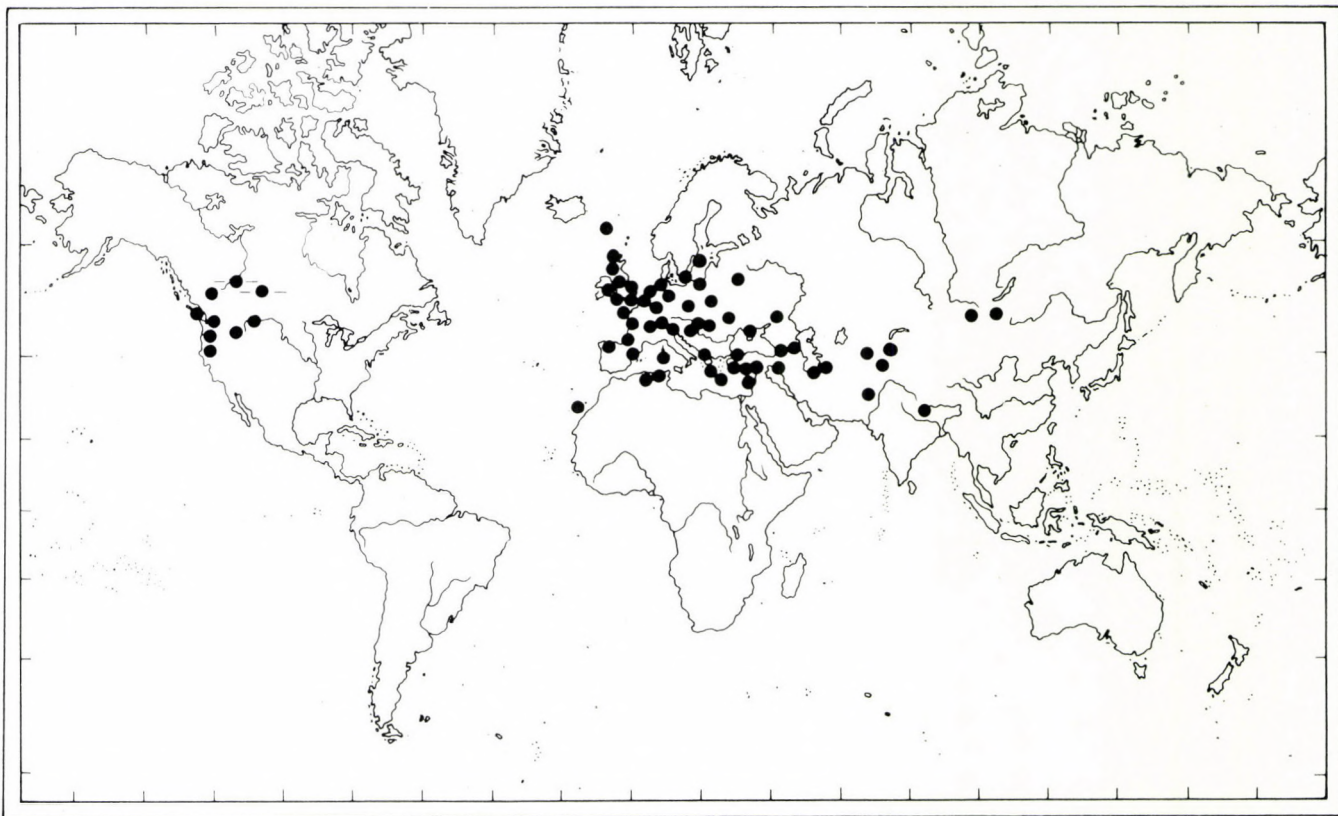



Fig. 12. The distribution of *T. ruraliformis* var. *ruraliformis* in the world

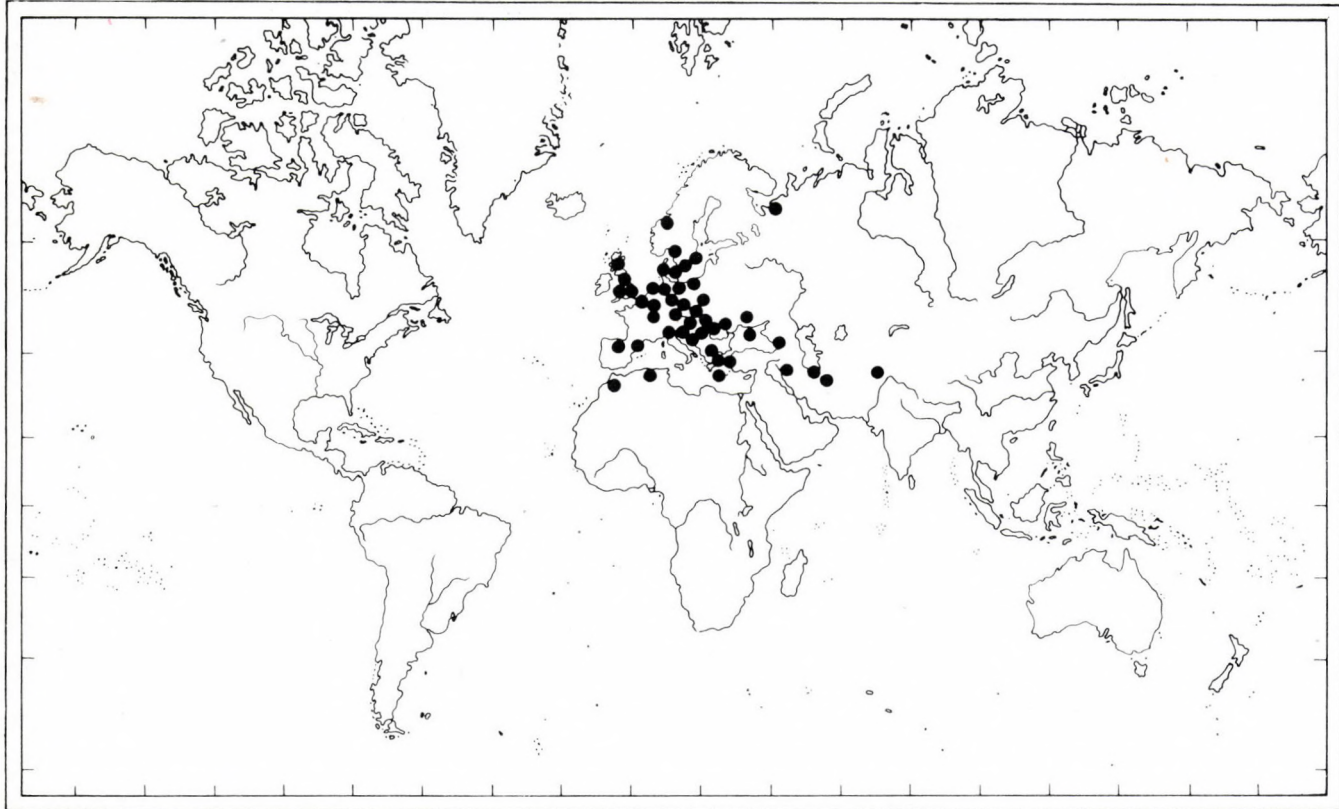



Fig. 13. The distribution of *T. virescens* ssp. *virescens* var. *virescens* in the world

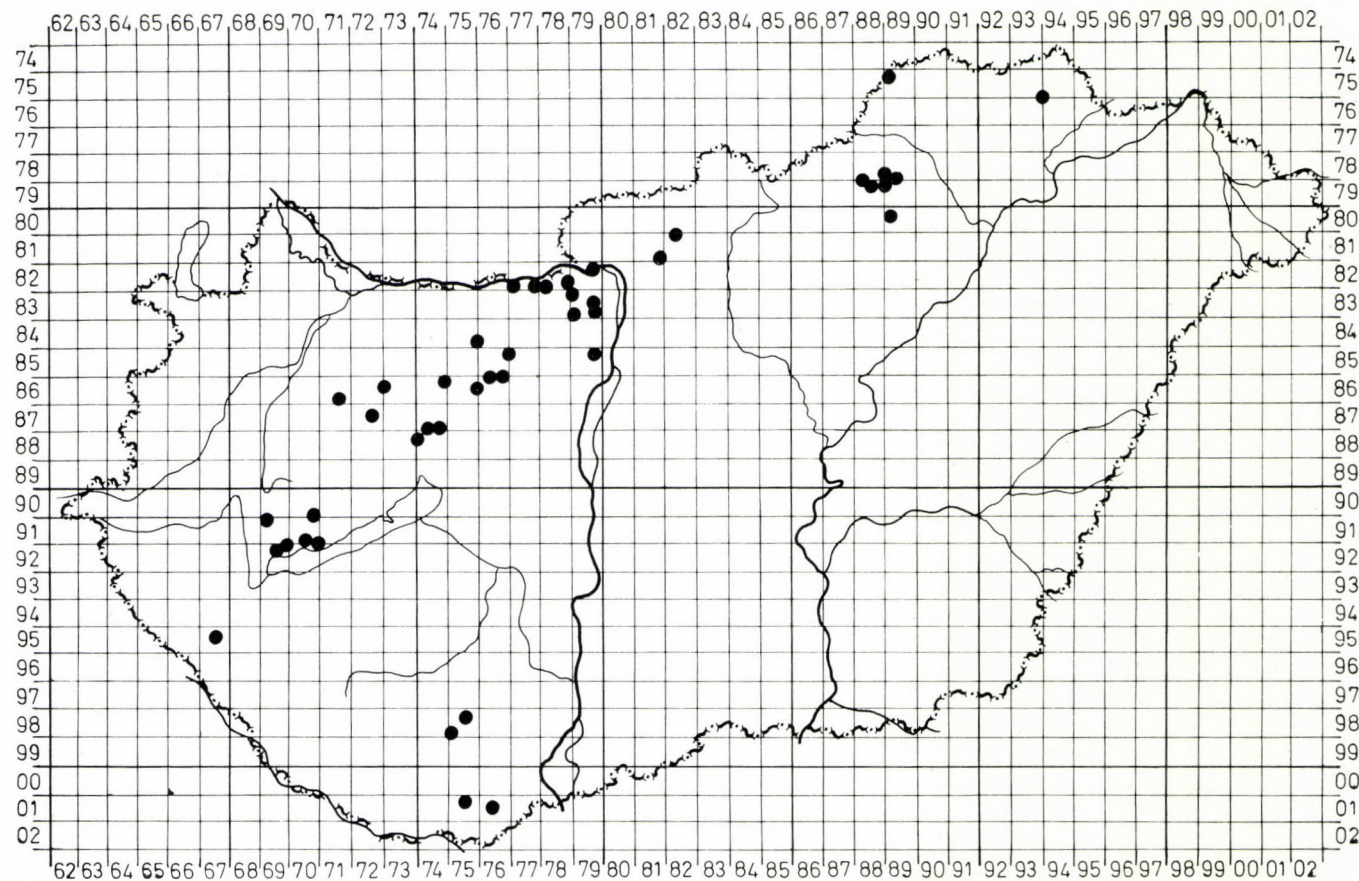



Fig. 14. The distribution of *T. calcicolens* in Hungary

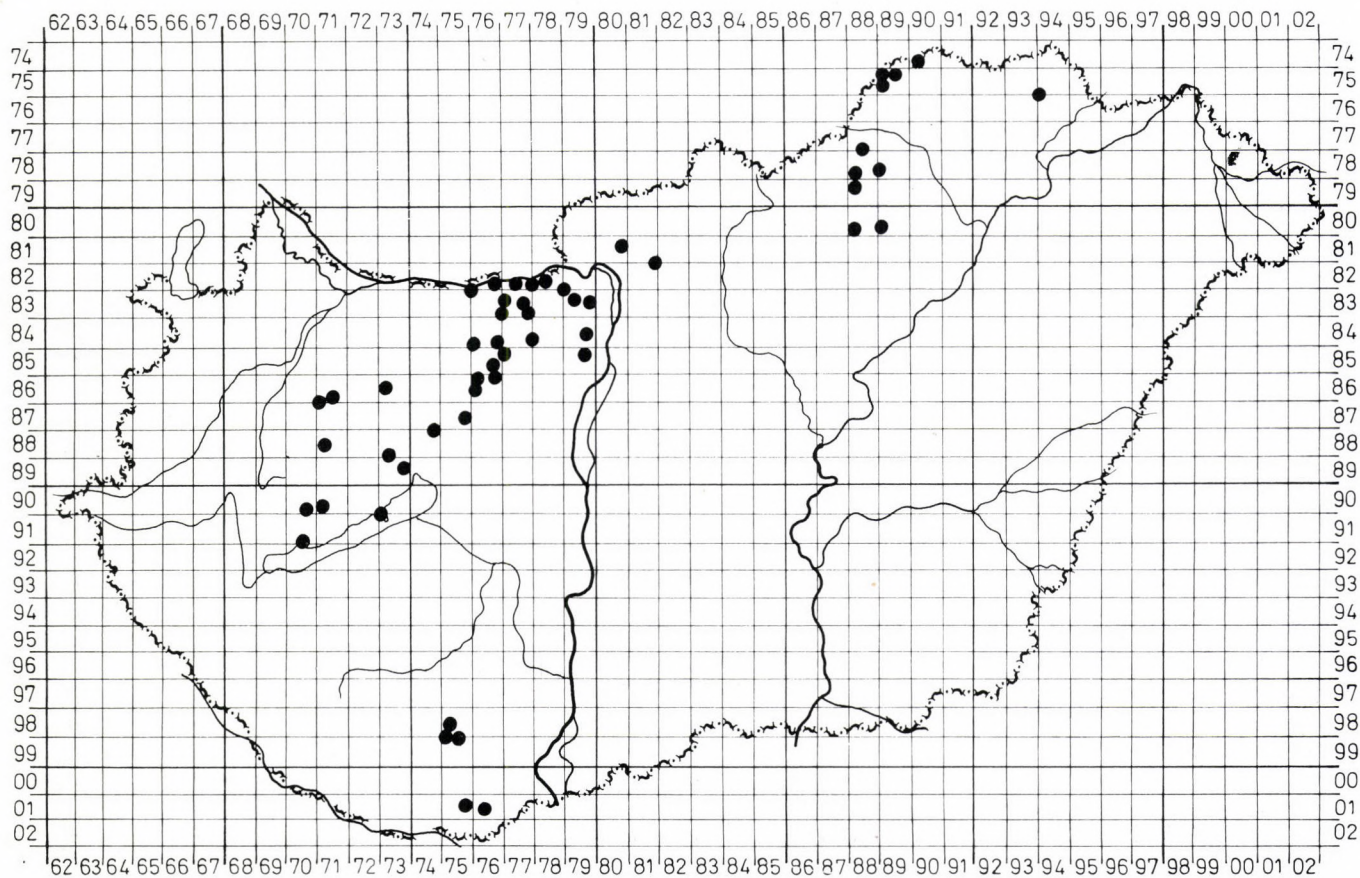



Fig. 15. The distribution of *T. intermedia* var. *intermedia* in Hungary

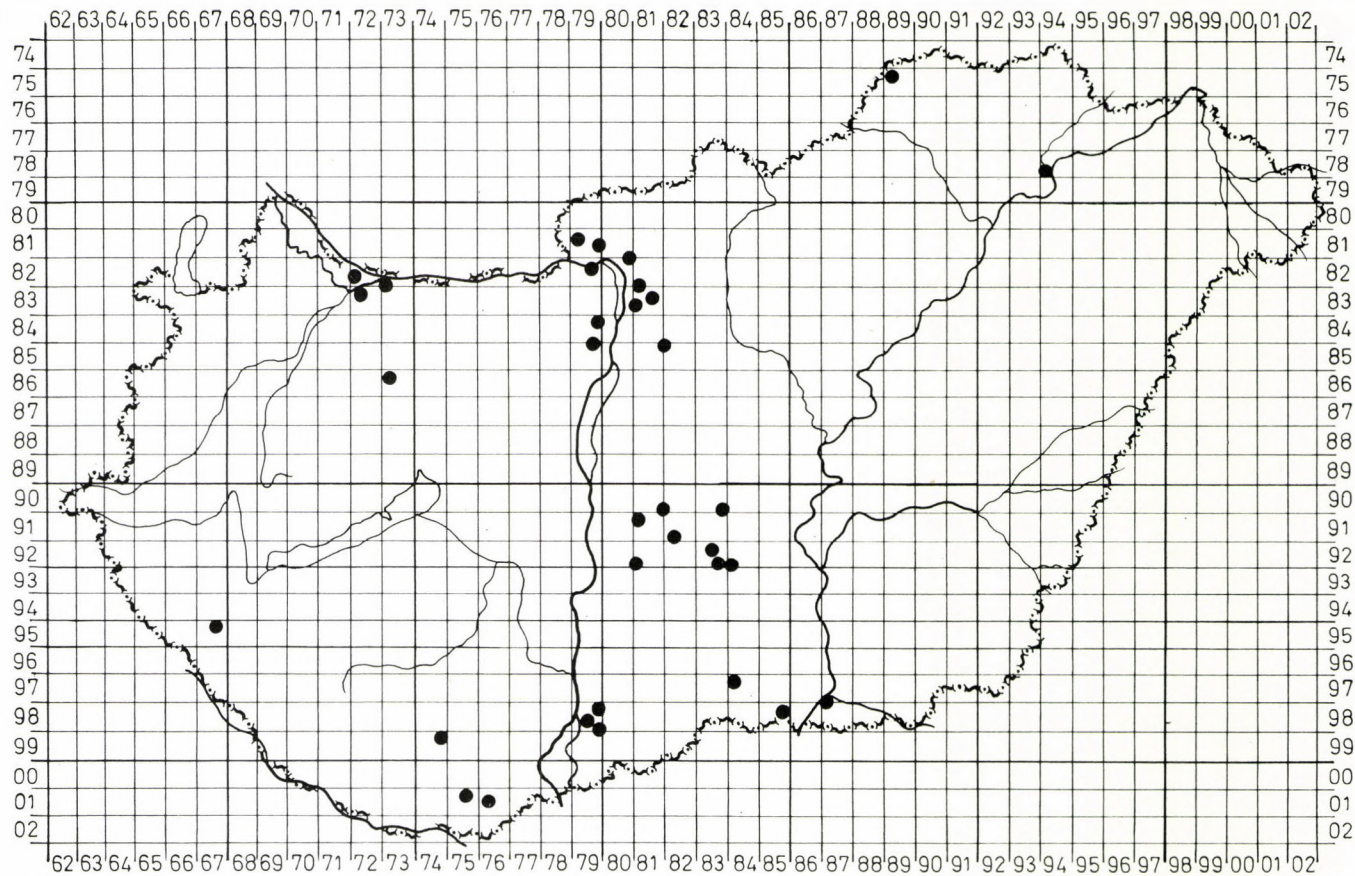



Fig. 16. The distribution of *T. ruralis* ssp. *hirsuta* var. *submamillosa* in Hungary

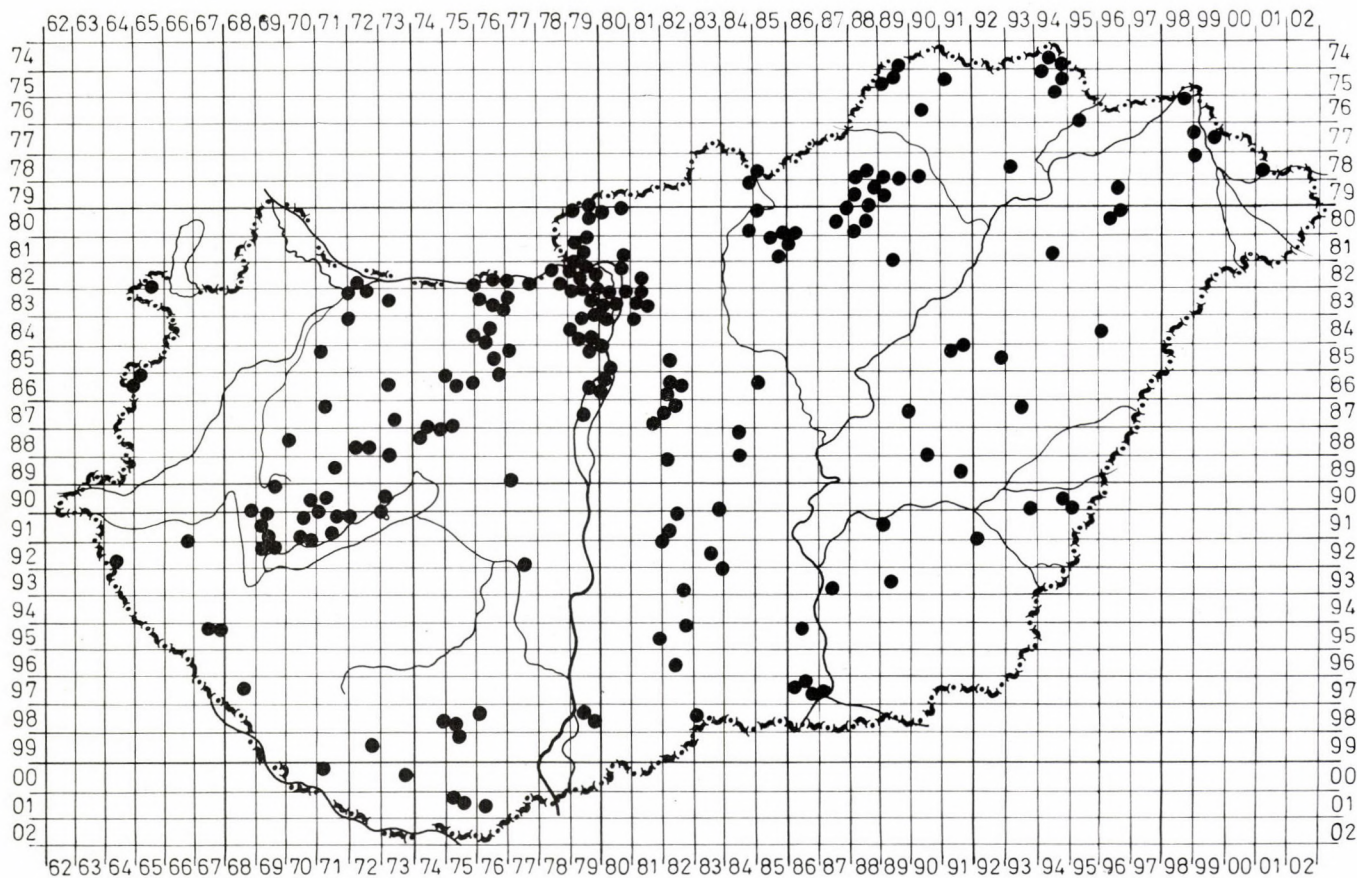



Fig. 17. The distribution of *T. ruralis* ssp. *ruralis* var. *ruralis* in Hungary

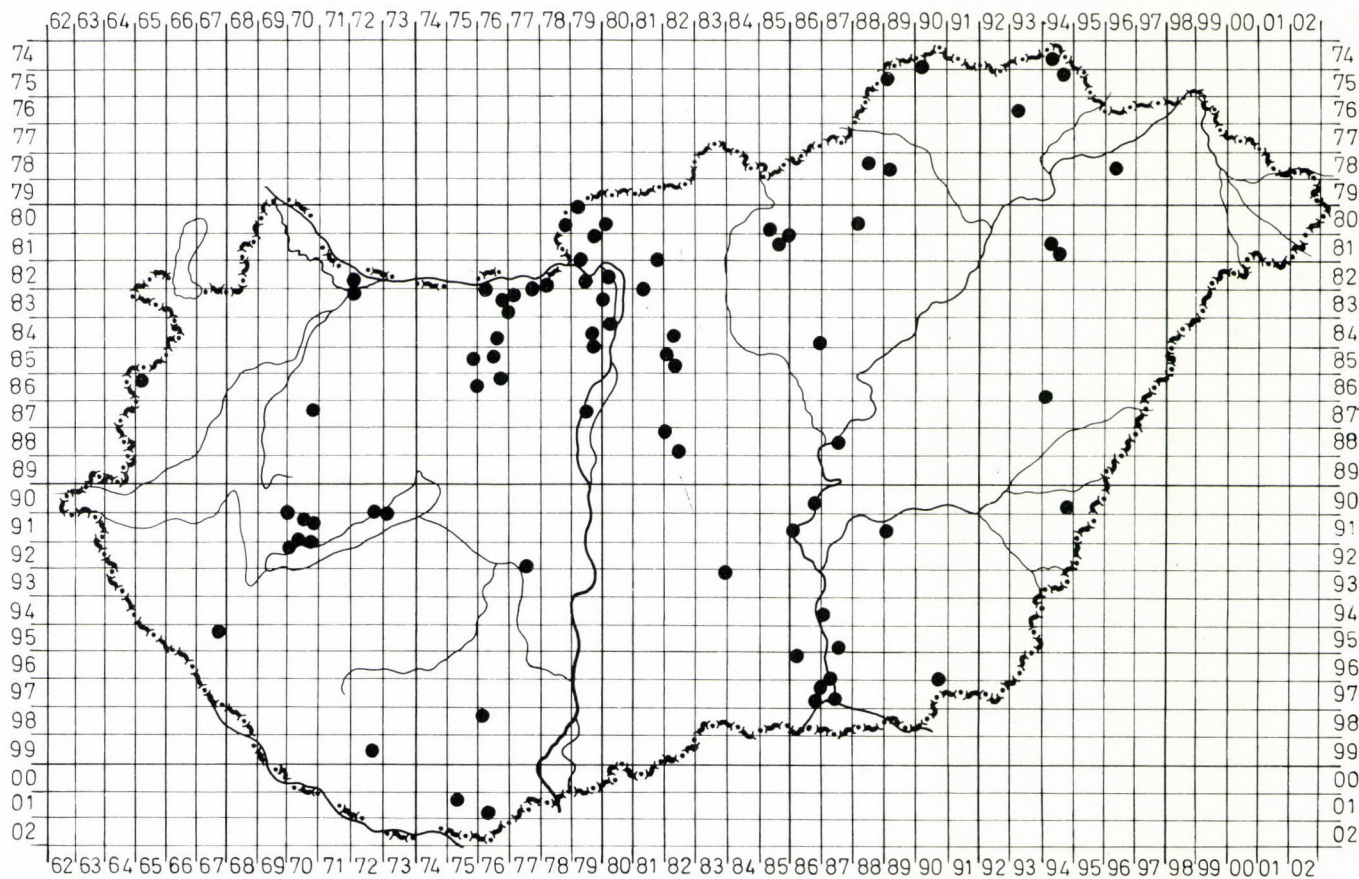



Fig. 18. The distribution of *T. virescens* ssp. *virescens* var. *virescens* in Hungary

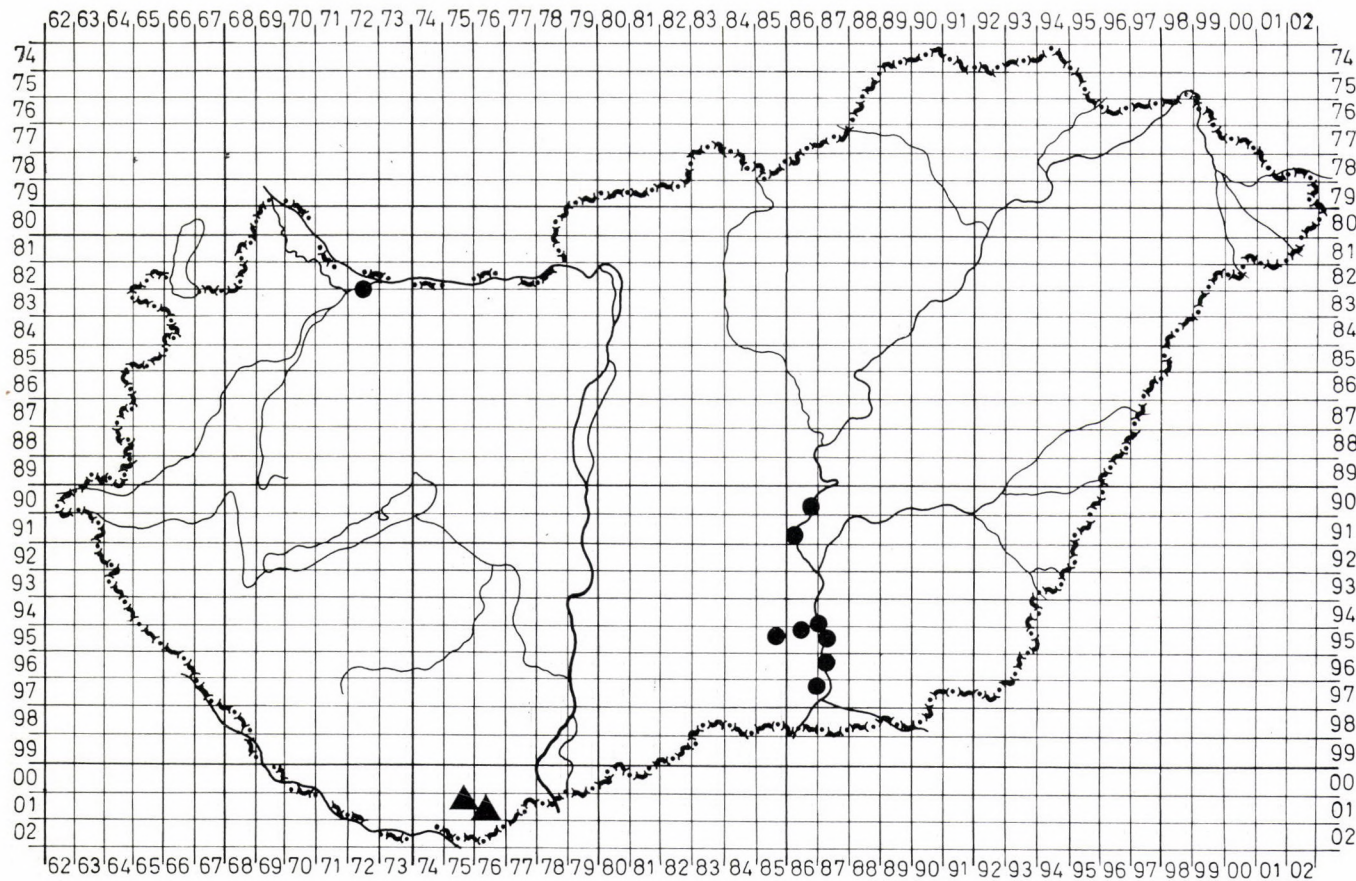



Fig. 19. The distribution of *T. princeps* (▲) and *T. latifolia* (●) in Hungary

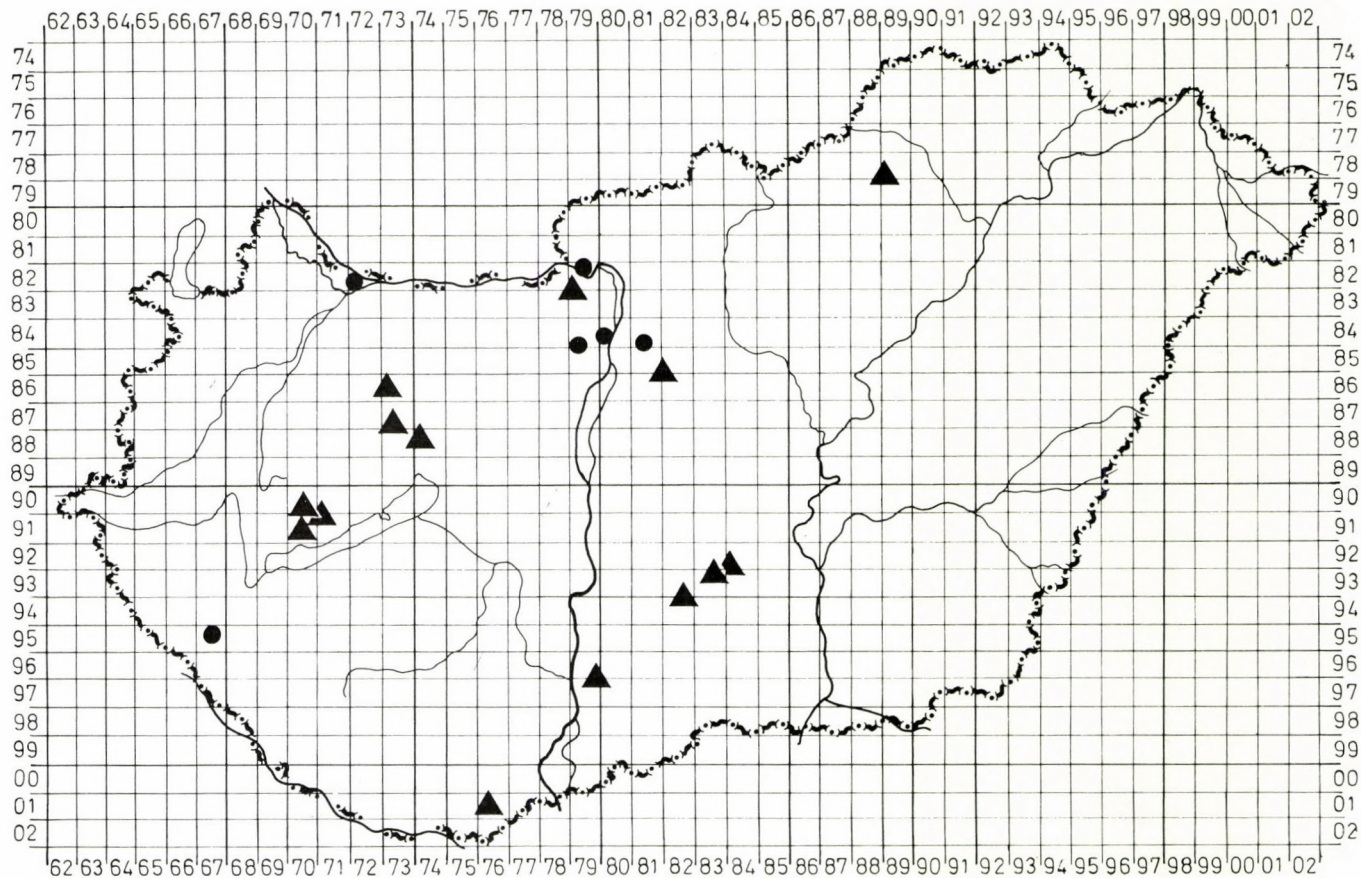



Fig. 20. The distribution of *T. ruraliformis* var. *ruraliformis* (▲) and *T. ruralis* ssp. *hirsuta* var. *hirsuta* (●) in Hungary

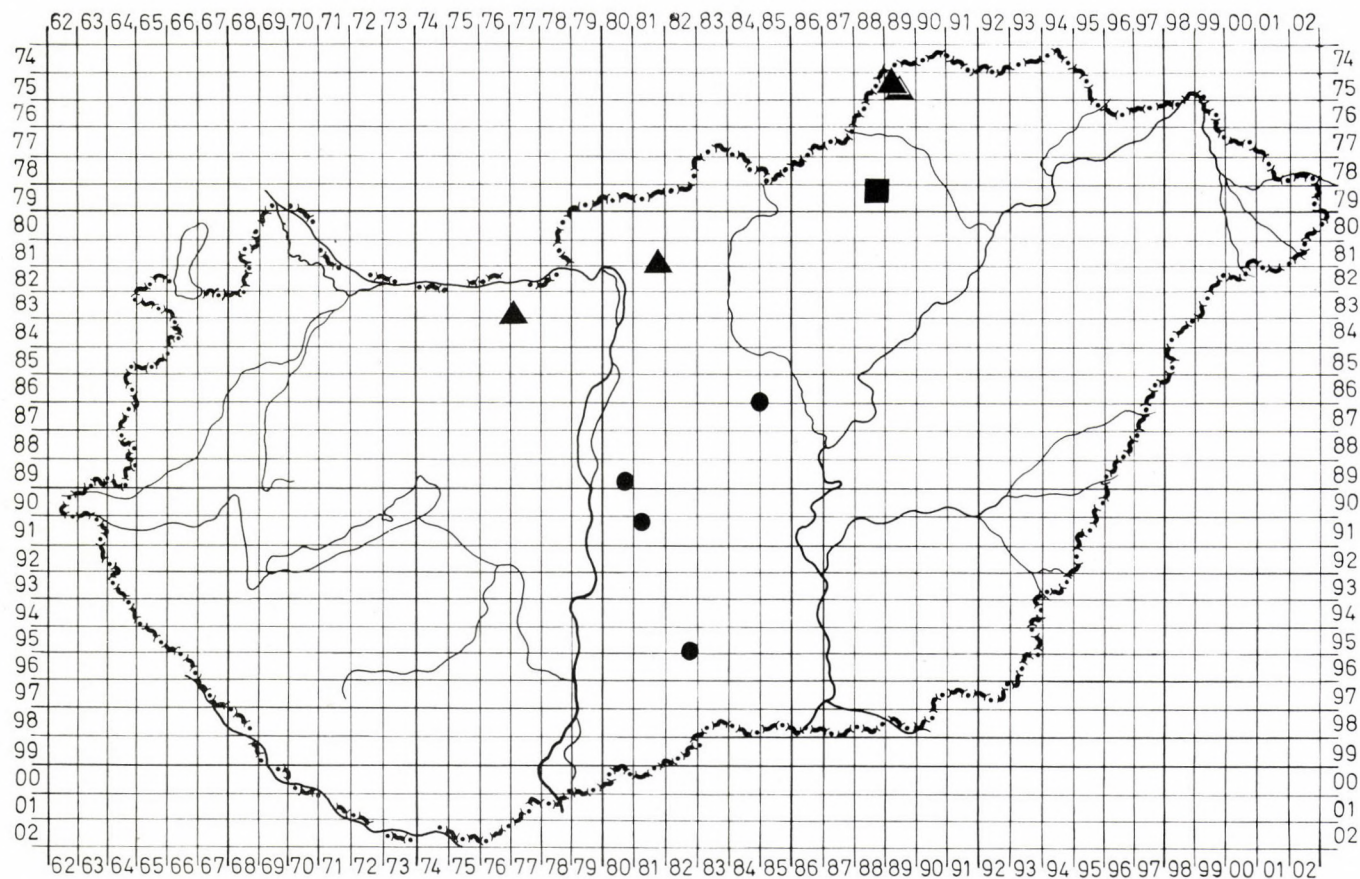



Fig. 21. The distribution of *T. norvegica* (■), *T. intermedia* var. *calva* (▲) and *T. caninervis* ssp. *spuria* var. *spuria* (●) in Hungary

ACKNOWLEDGEMENTS

I am grateful to L. MEINUNGER (Steinach, DDR) for the possibility to publish the new record of *Tortula norvegica* from the Bükk Mountains. Many thanks are due to T. PÓCS for his guidance during the whole study and his help in the identification of species and the preparation of this review. I thank the museum directors and curators of herbaria mentioned in the text for placing the *Tortula* specimens at my disposal.

BIBLIOGRAPHY

Including all works which contain distributional data.

Abramov, I. I., Abaczev, K. Ju. 1968: De Muscis Dagestaniae. *Nov. Sist. nizh. Rast.* **5:** 311–322.
Abramova, A. L., Abramov, I. I. 1959: De Muscis Armeniae. *Acta Instituti Botanici nom. V. L. Komarovii Acad. Sci. URSS. Ser. II., Plantae Cryptogamae, fasc.* **XII.,** 360–367.
Abramova, A. L., Abramov, I. I. 1964: Musci e Faucibus Kondara (Tadzhikistania). *Nov. Syst. Plant. non Vasc.* **1:** 325–341.
Abramova, A. L., Abramov, I. I. 1966: De Muscis Moldaviae. *Nov. Syst. Plant. non Vasc.* **3:** 315–326.
Abramova, A. L., Abramov, I. I. 1978: Materies ad Bryofloram Mongoliae II. *Nov. Syst. Plant. non Vasc.* **15:** 194–207.
Abramova, A. L., Tsegmed, Ts. 1982: Ad Bryofloram Montis Otgon-Tenger (Respublica Popularis Mongolia). *Nov. Syst. Plant. non Vasc.* **19:** 175–183.
Afonina, O. M., Bredkina, L. I., Makarova, I. I. 1979: Musci Lichenesque Zonae Silvo-Step-posae in fluxu medio Fl. Indigirka. *Nov. Syst. Plant. non Vasc.* **16:** 175–186.
Afonina, O. M., Perfiljeva, V. I. 1981: Musci partis Boreali-Orientalis Jakutiae (Distr. Verchojansk). *Nov. Syst. Plant. non Vasc.* **18:** 188–198.
Agnew, S., Vondrácek, M. 1975: A moss flora of Iraq. *Feddes Rep.* **86:** 341–489.
Ahti, T., Fagerstén, R. 1967: Mosses of British Columbia, especially Wells Gray Provincial Park. *Ann. Bot. Fenn.* **4:** 422–440.
Allorge, V. 1955: Catalogue préliminaire des Muscinées du Pays basque francis et espagnol. *Rev. Bryol. Lichénol.* **24:** 96–131.
Appleyard, J. 1970: A Bryophyte Flora of North Somerset. *Trans. Brit. Bryol. Soc.* **6:** 1–40.
Barriere, G., Comps, G., Letouzey-Dulau, L., Suire, C. 1978: Recherches écologique sur les Bryophytes des groupments forestiers du Sud-Ouest de la France. Les Bryophytes de la chenaie a *Quercus pubescens* du Quercy Septentrional et du Périgord Noir. *Rev. Bryol. Lichénol.* **44:** 53–70.
Bartram, E. B. 1949: Mosses of Guatemala. *Fieldiana: Botany* **25:** 442 pp.
Bartram, E. B. 1951: West Australian Mosses. *Trans. Brit. Bryol. Soc.* **1:** 465–470.
Birks, H. J. B., Birks, H. H. 1974: Studies on the bryophyte flora and vegetation of the Isle of Skye. I. Flora. *J. Bryol.* **8:** 197–254.
Bizot, M. 1955: Contribution à la flore bryologique d'Asie Mineure et de l'Ile de Cypre. *Rev. Bryol. Lichénol.* **24:** 69–72.
Bizot, M. 1965: Une poignée de mousses Romaines. *Bull. Mens. Soc. Linn. Lyon* **34:** 48–50.
Blagodatskich, L. S., 1979: Musci Frondosi in Systemate Fl. Kolyma superior crescentes. *Nov. Syst. Plant. non Vasc.* **16:** 186–194.
Boesen, D. F., Lewinsky, J., Rasmussen, L. 1975: A checklist of the bryophytes of the Faroes. *Lindbergia* **3:** 69–78.
Borbás, V. 1886: *A Magyar Homokpuszták Növényvilága meg a Homokkötés.* Budapest, 112 pp.
Borhidi, A., B. Thury, Zs., Zotter, F. J. 1968: Ground map and settlement list of Hungary for Flora Mapping of Central Europe. (In Hungarian). Bot. Gart. Univ. Budapest, 1–32.
Bornmüller, J. 1931: Zur Bryophyten-Flora Kleinasiens. *Magy. Bot. Lapok* **1(12):** 1–21.
Boros, Á. 1968: *Bryogeographie und Bryoflora Ungarns.* Akadémiai Kiadó, Budapest, 466 pp.
Bowers, F. D., Delgadillo, C. M., Sharp, A. J. 1976: The mosses of Baja California. *J. Hattori Bot. Lab.* **40:** 397–410.
Brassard, G. R., Fife, A. J., Weber, J. 1979: Mosses from Baffin Island, Arctic Canada. *Lindbergia* **5:** 99–104.
Brassard, G. R. 1983: Checklist of the mosses of the Island of Newfoundland, Canada. *Bryologist* **86:** 54–63.
Braun-Blanquet, J. 1954: Contribution à la flore bryologique du Maroc. *Rev. Bryol. Lichénol.* **23:** 100–104.
Brotherus, V. F. 1892: Enumeratio Muscorum Caucasi. *Acta Soc. Sci. Fennicae* **19:** 1–179.
Brotherus, V. F. 1928: Contribution à la flore bryologique du Cachemire. *Ann. Bryol.* **1:** 28–46.

Brughues, M. 1978: Flora briologica de los estratos del Buntsandstein de la Cordillera Costero Catalana. *Rev. Bryol. Lichénol.* **44:** 149–201.
Brühl, P. 1931: A census of Indian mosses. In: *Records of the Botanical Survey of India* 13/1. Calcutta, India, 135 pp.
Casas de Puig, C., Brugués, M. 1974: *Tortula ruralis* (Hedw.) Gaertn. var. *hirsuta* (Vent.) Par. (*Tortula papillosissima* (Copp.) Broth.) en Espagne. *Rev. Bryol. Lichénol.* **40:** 263–266.
Casas de Puig, C. 1975: Aportacion al estudio de la flora briologica espagnola. Musgos y Hepáticas de las provincias de Soria, Logrono, Burgos y Segovia. *Ann. Inst. Bot. Cavaniles* **32:** 731–762.
Casas Sicart, C. 1981: The mosses of Spain an annotated check-list. *Treballs de l'Institut Botanic de Barcelona*, 57 pp.
Chen, P.-Ch. 1941: Studien über die Ostasiatischen Arten der Pottiaceae I.—II. *Hedwigia* **80:** 1–76, 141–322.
Chorpa, R. S. 1975: Taxonomy of Indian mosses, *Botanical Monograph* 10. New Delhi, India, 631 pp.
Christy, J. A., Lyford, J. H., Wagner, D. H. 1982: Checklist of Oregon mosses. *Bryologist* **85:** 22–36.
Cridland, A. A. 1958: An Outline of the Bryophytes of County Laois (Queen's County). *Trans. Brit. Bryol. Soc.* **3:** 399–417.
Crum, H., Miller, H. A. 1956: Bryophytes from Guadalupe Island, Baja California. *The Southwestern Naturalist* **1:** 116–120.
Crum, H. 1964: Mosses of the Douglas Lake Region of Michigan. *The Michigan Botanist* **3:** 3–63.
Crum, H. 1966: Bryophytes of Owen Sound and the Bruce Peninsula, Ontario. *Nat. Mus. Canada Bull.* **216:** 102–122.
Crum, H., Kallio, P. 1966: Bryophytes of Labrador and Ungava. *Nat. Mus. Canada Bull.* **216:** 87–101.
Crum, H. 1972: Mosses new to the State of Michigan. *The Michigan Botanist* **11:** 123–124.
Crum, H., Steere, W. C., Anderson, L. E. 1973: A new list of mosses of North America, North of Mexico. *Bryologist* **76:** 85–130.
Crum, H., Steere, W. C. 1981: Mosses of Eastern North America I.—II. Columbia University Press, New York, 1328 pp.
Crundwell, A. C. 1968–1971: New vice-county records and amendements to the Census Catalogue. *Trans. Brit. Bryol. Soc.* **5:** 629–649, 876–892, **6:** 374–384.
Damsholt, K., Holmen, K., Warncke, E. 1969: A list of the Bryophytes of Denmark. *Bot. Tid.* **65:** 163–183.
Demaret, F., Castagne, É. 1964: Bryophytes. In: *Flora Générale de Belgique* (ed. W. Robins), Bruxelles, **2/3:** 233–397.
Dhien, R. 1981: Florule bryologique des rochers bathoniens. *Cryptog., Bryol. Lichénol.* **2:** 233–234.
Douglas, G. W., Vitt, D. H. 1976: Moss-Lichen Flora of St. Elias-Kluane Ranges, Southwestern Yukon. *Bryologist* **79:** 437–456.
Duncan, U. K. 1956: A Bryophyte Flora of Wigtownshire. *Trans. Brit. Bryol. Soc.* **3:** 50–63.
Duncan, U. K. 1966: A Bryophyte Flora of Angus. *Trans. Brit. Bryol. Soc.* **5:** 1–82.
Dupret, H. 1934: Études sur Mousses de la région de Montréal. *Contrib. Lab. Bot. Univ. Montréal*, **25.,** 70 pp.
Düll, R., Düll-Hermanns, I. 1973: Ergänzungen und Nachträge zur Bryoflora und Bryogeographie der ostmediterranen Insel Kreta in der Aegaeis. *J. Bryol.* **7:** 421–437.
Düll, R. 1979: Neue Übersicht zur Moosflora der Insel Kreta (Aegaeis). *J. Bryol.* **10:** 491–509.
Düll, R. 1980: Die Moose (Bryophyta) des Rheinlandes (Nordhein-Westfalen, Bundesrepublik Deutschland). *Decheniana-Beihefte (Bonn)* **24:** 1–365.
Eggers, J. 1982: Artenliste der Moose Makaronensiens. *Cryptog., Bryol. Lichénol.* 3: 283–336.
Fitzgerald, J. W., Fitzgerald, R. D. 1960: A Bryophyte Flora of Co. Tyrone. *Trans. Brit. Bryol. Soc* **.3:** 653–687.
Frahm, J.-P. 1978: Zur Moosflora der Sahara. *Nova Hedwigia* **30:** 527–548.
Frey, W., Kürschner, H. 1983: New records of bryophytes from Transjordan with remarks on phytogeography and endemism in SW Asiatic mosses. *Lindbergia* **9:** 121–132.
Froehlich, J. 1950: Bryophyten aus Iran. *Ann. Naturhist. Mus. Wien* **57:** 37–41.
Froehlich, J. 1964: Bryophyten aus Afghanistan und Nordwest-Pakistan. *Ann. Naturhist. Mus. Wien* **67:** 149–158.
Gangulee, H. C. 1972: Mosses of Eastern India and Adjacent Regions. III. Pottiales. Calcutta, India, 624–784.

Gardiner, J. C. 1981: A bryophyte flora of Surrey. *J. Bryol.* **11:** 747–842.
Geissler, P. 1977: Zur Moos- und Flechtenflora Nordgriechenlands. *Bauhinia* **6:** 189–213.
Geissler, P. 1979: Bryologische Notizen aus den Picos de Europa (Nordspanien). *Mém. Soc. Bot. Genève* **1:** 131–136.
Grolle, R., Meinunger, L., Hilbig, W., Huneck, S. 1983: Beitrag zur Kenntnis der Moosflora der Mongolischen Volksrepublik. *Feddes Rep.* **94:** 107–124.
Győrffy, I. 1943: A nagybugaci erdő borókásairól. *Természettud. Közl. Pótf.* 1943. júl–szept: 1–10.
Haapasari, M. 1966: Sammaltietoja keski-Kittilästä (Lk). *Mem. Soc. Fauna Flora Fenn.* **42:** 27–41.
Harthill, M. P., Long, D. M., Mishler, B. D. 1979: Preliminary List of Southern California Mosses. *Bryologist* **82:** 260–266.
Hébrard, J. P. 1968: Apercu sur la vegetation muscinale des montagnes calcaires dans la province italienne des Abruzzes. *Rev. Bryol. Lichénol.* **44:** 7–46.
Hébrard, J. P. 1980: Contribution à l'étude des muscinées du Parc National des Écrins. Observations floristiques et écologiques. *Cryptog., Bryol. Lichénol.* **1:** 339–397.
Holmen, K., Scotter, G. W. 1971: Mosses of the Reindeer Preserve. *Lindbergia* **1:** 34–56.
Hübschmann, A. von 1978: Über Moosvegetation und Moosgesellschaften der Insel Vancouver (Kanada). *Phytocoenologia* **5:** 80–123.
Ireland, R. R., Bird, C. D., Brassard, G. R., Schofield, W. B., Vitt, D. H. 1980: Checklist of the mosses of Canada. *Nat. Mus. Canada, Publ. Bot.* **8.,** Ottawa, 75 pp.
Iwatsuki, Z., Noguchi, A. 1973: Index Muscorum Japonicarum. *J. Hattori Bot. Lab.* **37:** 299–418.
Iwatsuki, Z., Noguchi, A. 1979: Index Muscorum Japonicarum. Supplement 1973–1978. *J. Hattori Bot. Lab.* **46:** 235–255.
Jäderholm, E. 1902: Einige Beiträge zur Kenntnis der transkaukasischen Moosflora. *Hedwigia* **41:** 84–88.
Jelenc, F. 1955: Muscinées de l'Afrique du Nord (Algerie, Tunisie, Maroc, Sahara). *Bull. Soc. Geogr. Arch. Oran* **72–76:** 1–152.
Jelenc, F. 1967: Muscinées de l'Afrique du Nord (Supplement). *Rev. Bryol. Lichénol.* **35:** 186–215.
Jelenc, F. 1973: Les Bryophytes du bassin de la Vienne. 3[e] fascicule: Bryophytes du Département de la Haute-Vienne de l'herbier Charles Le Gendre. *Rev. Bryol. Lichénol.* **39:** 630–660.
Jones, E. W. 1946: Notes on the bryophyte flora of Grímsey and other parts of North Iceland. *Bryologist* **49:** 14–29.
Jones, E. W. 1953: A Bryophyte Flora of Berkshire and Oxfordshire. II. Musci. *Trans. Brit. Bryol. Soc.* **2:** 220–277.
Juratzka, J., Milde, J. 1870: Beitrag zur Moosflora des Orientes. Kleinasien, das westliche Persien und den Caucasus umfassend. *Verh. Zool.-bot. Ges. Wien* **20:** 589–602.
Karzmarz, K., Kuc, M. 1962: The mosses of the eastern part of the Lublin Upland. *Fragm. Flor. Geobot.* **8:** 483–508.
Karzmarz, K., Świes, F. 1981: Beitrag zur Bryoflora der Mongolei 1. Laub- und Lebermoose aus dem Chentei-Gebirge. *Feddes Rep.* **92:** 695–711.
Kárpáti, I., Vajda, L. 1961: Beiträge zur Moosflora Albaniens. *Fragm. Bot.* **1:** 3–16.
Kilbertus, G., Bizot, M. 1971: Contribution à la connaissance de la flore des muscines d'Afghanistan. *Bull. Acad. Soc. Lorraines des Sci.* **10:** 67–75.
Koponen, T., Suominen, J. 1965: Mosses from the rock faces in Lammi commune, southern Finland. *Mem. Soc. Fauna Flora Fenn.* **41:** 42–58.
Koppe, F. 1964: Die Moose des Niedersächsichen Tieflandes. *Abh. naturw. Ver. Bremen* **36:** 237–424.
Koppe, F. 1965: Bryologische Beobachtungen auf der Insel Mallorca. *Bot. Not.* **118:** 25–48.
Koppe, F. 1971: Bryofloristische Beobachtungen auf der Insel Langeoog. *Natur und Heimat* **31:** 113–134.
Koppe, F., Koppe, K. 1972: Bryofloristische Beobachtungen im westheinischen Bergland. *Decheniana* **125:** 79–102.
Koppe, F. 1976: Beobachtungen über die Moosvegetation und Moosflora von Zypern. *Herzogia* **4:** 95–136.
Koppe, F., Duell, R. 1982: Beiträge zur Bryologie und Bryogeographie von Tenerife. *Bryol. Beitr.* **1:** 37–107.
Kramer, W. 1980: Tortula Hedw. sect. Rurales De Not. (Pottiaceae, Musci) in der östlichen Holarktis. *Bryoph. Bibl.* **21.** J. Kramer, Vaduz, 165 pp.
Kuc, M. 1959: The mosses of the Sandomierz-Opatów Upland. *Fragm. Flor. Geobot.* **5:** 129–150.
Kuc, M. 1959: Bryological records from the district of Staszów. *Fragm. Flor. Geobot.* **5:** 287–297.

Kuc, M. 1962: Mousses de la partie ouest du plateau de Lublin (Pologne orientale). *Fragm. Flor. Geobot.* **8:** 23–55.
Kuc, M. 1963: Bryophyta from the northwest of Sorkapp Land, Vestspitzbergen. *Norsk Polarinstitutt, Oslo,* 140–145.
Kuc, M. 1973: Addition to the arctic moss flora. VI. Moss flora of Masik River valley (Banks Island) and its relationship with plant formations and the Postglacial history. *Rev. Bryol. Lichénol.* **39:** 253–264.
Kuc, M. 1973: A review of the mosses of Svalbard. *Rev. Bryol. Lichénol.* **39:** 401–472.
Kuc, M. 1973: Addition to the arctic moss flora. VII. Altitudinal differentiation of the moss cover at Purchase Bay, Melville Island, N. W. T. *Rev. Bryol. Lichénol.* **39:** 539–553.
Kuc, M. 1973: Bryogeography of expedition area, Axel Heiberg Island, N. W. T., Canada. *Bryoph. Bibl.* **2.,** J. Kramer, Vaduz, 120 pp.
Kujala, V., Fagerström, L., Ulvinen, A. 1979: Die Laubmoose in Kymenlaakso in Südfinland. *Acta Bot. Fenn.* **109:** 1–34.
Lasala, E. F., Fernandez, M. L. L. 1976: Flora briofitica de la Sierra de Codes. *Rev. Bryol. Lichénol.* **42:** 715–730.
Lawton, E. 1971: Moss flora of the Pacific Northwest. *The Hattori Botanical Laboratory, Nichinan, Miyazaki,* Japan, 362 pp.
Lewinsky, J. 1971: Mosses of the Skjoldungen Area, Southeast Greenland. *Linbergia* **1:** 83–90.
Lewinsky, J. 1974: Some new or noteworthly mosses from West Greenland. *Bryologist* **77:** 74–77.
Lisowski, S. 1956: Mchy Bieszczadów Zachodnich. *Pozn. Tow. Przyj. Nauk, Wydz. Mat. Przyrod., Prace Komisji Biol.* **17:** 1–94.
Lisowski, S. 1959: Materialy do Bryoflory Tatr. *Pozn. Tow. Przyj. Nauk, Wydz. Mat. Przyrod., Prace Komisji Biol.* **21:** 21–149.
Lo Guidice, R., Privitera, M. 1979: La flora muscinale della valle S. Giacomo (Etna). *Rev. Bryol. Lichénol.* **45:** 453–466.
Long, D. G., Crundwell, A. C., Townsend, C. C. 1981: New records of bryophytes from the Canary Islands. *J. Bryol.* **11:** 521–536.
Magill, R. E. 1981: *Flora of Southern Africa* wich deals with the territories of South Africa, Transkei, Lesotho, Swaziland, Baphuthatswana, South West Africa/Namibia, Botswana and Venda. Bryophyta part I. Mosses, Fascicle 1, Sphagnaceae — Grimmiaceae. Botanical Research Institute, Department of Agriculture and Fisheries, Republic of South Africa, 291 pp.
Mahler, B. D., Mahler, W. F. 1980: Checklist of Mosses of Oklahoma. *Bryologist* **83:** 202–208.
Meinunger, L. 1971: Zur Moosflora von Südthüringen. 3. Beitrag. *Wiss. Z. Univ. Halle, math-nat.* **21:** 37–42.
Meylan, Ch. 1940: Contribution à la connaissance de la flore bryologique de l'Islande. *Bull. Soc. Bot. Suisse* **50:** 475–499.
Miller, N. G., Halbert, R. L. 1971: A collection of bryophytes from Summer Island, Delta County, Michigan. *The Michigan Botanist* **10:** 3–13.
Miller, N. G., Ireland, R. R. 1978: A floristic account of the bryophytes of Bathrust Island, Arctic Canada. *Occasional papers of the Farlow Herbarium of Harward University,* **13,** 38 pp.
Miller, H. A., Whittier, H. O., Whittier, B. A. 1978: Prodromus Florae Muscorum Polynesiae. *Bryoph. Bibl.* **16,** J. Kramer, Vaduz, 334 pp.
Mogensen, G. S., Lewinsky, J. 1982: Distribution maps of bryophytes in Greenland 8. *Lindbergia* **8:** 125–128.
New vice-county records. *Trans. Brit. Bryol. Soc.* **1:** 26–35, 374–388, **2:** 89–108, **3:** 322–338, 461–490, 763–782.
Nichols, G. E. 1937: Bryophytes of the Purcupine Mountains, Ontonagon County, Michigan. *Papers of the Mich. Acad. Sci., Arts and Letters* **22:** 183–200.
Nichols, G. E. 1938: Bryophytes of the Huron Mountain Region, Marquette County, Michigan. *Bryologist* **41:** 25–31.
Nyholm, E. 1956: Musci II. Fasc. II. Illustrated Moss flora of Fennoscandia. *CWK Gleerup, Lund Sweden, Malmö,* 85–189.
Ochyra, R. 1976: Materials to the bryoflora of Southern Poland. *Zeszyty Naukowe Unigersytetu Jagellonskiego, Prace Bot.* **4:** 107–125.
Ochyra, R. 1978, 1980, 1981: Musci Poloniae Exsiccati, Centuria I., III., V. *Fragm. Flor. Geobot.* **24:** 331–356, **26:** 189–242, 367–418.
Ochyra, R., Pacyna, A. 1980: A contribution to the moss flora of Mongolia. *Fragm. Flor. Geobot.* **26:** 75.
Ochyra, R. 1984: Moss flora of the Nowotarskie and Spiskie Klippen (Pieniny Klippen Belt, Western Carpathian Mts.). *Fragm. Flor. Geobot.* **28:** 419–489.

Paton, J. A. 1961: Bryophyte flora of South Hants. *Trans. Brit. Bryol. Soc.* **4:** 1–83.
Paton, J. A. 1969: A bryophyte flora of Cornwall. *Trans. Brit. Bryol. Soc.* **5:** 669–756.
Paton, J. A., Crundwell, A. C. 1974: New vice-county records and amendements to the Census Catalogue. *J. Bryol.* **8:** 161–176.
Pavletić, Z. 1955: *Prodromus Flore Briofita Jugoslavije.* Jugoslavenska Akademija Znanosti i Umjetnosti, Zagreb, 578 pp.
Perry, A. R. 1967: New vice-county records and amendements to the Census Catalogue. *Trans. Brit. Bryol. Soc.* **5:** 405–425.
Persson, H., Weber, W. A. 1958: The bryophyte flora of Mt. McKinley National Park, Alaska. *Bryologist* **61:** 214—242.
Persson, H., Holmen, K. 1961: Bryophytes collected during the Arctic Field Trip of the Ninth International Botanical Congress. *Bryologist* **64:** 179–198.
Persson, H. 1962: Bryophytes from Alaska collected by E. Hultén and others. *Svensk Bot. Tid.* **56:** 1–35.
Persson, H. 1963: Bryophytes of Alaska and Yukon Territory collected by T. Shacklette. *Bryologist* **66:** 1–26.
Persson, H., Viereck, L. A. 1983: Collection of some bryophytes from Alaska. *Lindbergia* **9:** 5–20.
Peterson, W. L., Smith, D. K., Sharp, A. J. 1980: The mosses of the Kodiak Archipelago. *J. Hattori Bot. Lab.* **47:** 269–285.
Petrov, S. 1975: *Bryophyta Bulgarica clavis Diagnostica.* Acad. Sci. Bulg., Sofia, 536 pp.
Pierrot, R. B. 1974: Comptes-rendus des sorties bryologique 1974. *Bull. Soc. Bot. du Centre-Ouest, nonv. série* **5:** 109–111.
Piippo, S. 1981: Nåtön (Al: Lemland) sammalkasvistosa. *Mem. Soc. Fauna Flora Fenn.* **57:** 101–108.
Piippo, S. 1982: The bryophyte flora of Tammisto Nature Reserve, S. Finland. *Mem. Soc. Fauna Flora Fenn.* **58:** 61–64.
Podpera, J. 1954: *Conspectus Muscorum Europaeorum.* Ceskoslov. Akademie Ved, Praha, 697 pp.
Pospisil, V. 1961: Die Moosflora im einzugsgebiet der Oberen Topla in den Karpathen. *Acta Musei Moraviae* **46:** 101–152.
Pospisil, V. 1979: Laubmoosflora an der Mittleren Jihlava. *Acta Musei Moraviae* **64:** 37–64.
Preston, C. D., Akeroyd, J. R. 1979: A bryophyte collection from Mt. Olympus, Thessaly, Greece. *Rev. Bryol. Lichénol.* **45:** 437–442.
Preston, C. D. 1984: A check-list of greek mosses. *J. Bryol.* **13:** 43–96.
Privitera, M., Lo Guidice, R. 1981: Vegetazione muscinale della faggeta del bosco di Malabotta (Peloritani). *Cryptog., Bryol Lichénol.* **2:** 181–200.
Proctor, M. C. F. 1956: A bryophyte flora of Cambridgeshire. *Trans. Brit. Bryol. Soc.* **3:** 1–49.
Proctor, M. C. F. 1960: Mosses and liverworts of the Malham District. *Field Studies* **1:** 1–25.
Rallet, R. 1966: Catalogue des muscinées du département des Deux-Sevres. *Rev. Féd. Franc. Soc. Sci. Nat., Ser.* 3, **5/19:** 1–50.
Rajczy, M. 1979: Contribution to the bryoflora of Greece, I. The bryophytes of the Cave Perama near Joannina. *Stud. Bot. Hung.* **13:** 3–5.
Ricek, E. W. 1977: *Die Moosflora des Attergaues, Hausruck- und Kobernanserwaldes.* Oberösterreichischer Musealverein, Linz, 243 pp.
Rilstone, F. 1948: A bryophyte flora of Cornwall. I. Musci. *Trans. Brit. Bryol. Soc.* **1:** 75–100.
Robinson, H., Godfrey, R. K. 1960: Contribution to the bryophyte flora of Turkey. *Rev. Bryol. Lichénol.* **29:** 244–253.
Rose, F. 1951: A bryophyte flora of Kent. III. Musci. *Trans. Brit. Bryol. Soc.* **1:** 427–464.
Rusińska, A. 1981: Mchy Pojezierza Kartuskiego. *Pozn. Tow. Przyj. Nauk, Wydz. Mat. Przyrod., Prace Komisji Biol.* **59:** 1–153.
Sainsbury, G. O. K. 1955: A handbook of the New Zealand mosses. *R. Soc. New Zealand Bull.* **5,** 490 pp.
Saito, K. 1975: A Monograph of japanese Pottiaceae (Musci). *J. Hattori Bot. Lab.* **39:** 373–537.
Savicz-Ljubitzkaja, L. I., Smirnova, Z. N. 1970: *The Handbook of the Mosses of the U.S.S.R.* The mosses Acrocarpous. Nauka, Leningrad, 824 pp.
Sayre, G. 1940: Mosses of the Santa Barbara Islands. *Bryologist* **43:** 32–35.
Schiffner, V. 1897: Bryologische Mittheilungen aus Mittelböhmen. *Österr. Bot. Zeitschr.* **47:** 54–59.
Schiffner, V. 1897: Musci Bornmülleriani. *Österr. Bot. Zeitschr.* **47:** 125–132.
Schofield, W. B. 1968: A selectively annotated checklist of British Columbia mosses. *Syesis* **1:** 163–175.

Schubert, R., Schubert, W., Koperski, M. 1977: Beitrag zur Moosflora der Mongolischen Volksrepublik. *Feddes Rep.* **88:** 81–102.
Scott, G. A. M., Stone, I. G. 1976: *The Mosses of Southern Australia.* Academic Press, London, New York, San Francisco, 495 pp.
Showers, D. V. 1982: The mosses of Lassen Volcanic National Park, California. *Bryologist* **85:** 324–328.
Sim. T. R. 1926: The Bryophyta of South Africa, comprising Sphaerocarpales, Marchantiales, Anthocerotales, Sphagnales, Polytrichales, Bryales. *Trans. R. Soc. S. Afr.* **15:** 1–475.
Simon, T., Kovács-Láng, E. 1972: Produkcióbiológiai vizsgálatok a csévharaszti IBP mintaterületen. *MTA Biol. Oszt. Közl.* **15:** 61–69.
Simon, T., Szerényi, G. 1975: Moss ecological investigation in forest-steppe associations of the IBP-area at Csévharaszt. *Acta Bot. Acad. Sci. Hung.* **21:** 117–136.
Simon, T., Kovács-Láng. E. 1976: Phytomass production and environmental conditions of grassland on sand soil at Csévharaszt (IBP experimental area in Hungary). *Pol. Ecol. Stud.* **2:** 121–127.
Sloover, J.-L. 1976: Bryophytes des Iles de la Madeleine (Québec, Canada). *Lejeunia (Revue de Botanique), N. Sér.* **80:** 1–9.
Smarda, J. 1946: Vysledky bryogeografickych studii na Moravé. *Čas. Morav. zemsk. mus. Brno* **30:** 41–77.
Smarda, J. 1948: The mosses of Slovakia (ČSR). *Čas. Morav. zemsk. mus. Brno* **32:** 1–75.
Smarda, J. 1952: Prvni doplnek k „Mechum Slovenska". *Acta Musei Moraviae* **37:** 102–127.
Smith, A. J. E. 1964: A bryophyte flora of Glamorgan. *Trans. Brit. Bryol. Soc.* **4:** 539–596.
Smith, A. J. E. 1978: *The Moss Flora of Britain and Ireland.* Cambridge University Press, Cambridge, London, New York, Melbourne, 706 pp.
Sollman, Ph. 1983: De Mosflora van Noordelijk Friesland. *Lindbergia* **9:** 186–188.
Sollman, Ph. 1983: De mosflora van Kerkhoven in Oost-Gelderland. *Lindbergia* **9:** 190–191.
Soó, R. 1956: Conspectus des groupments végétaux dans les Bassin Carpathiques. II. Les associations psammophiles et leur génétique. *Acta Bot. Acad. Sci. Hung.* **19,** Suppl. p. 529.
Stark, L. R., Castetter, R. C. 1982: A preliminary list of bryophytes from the Organ Mountains, New Mexico. *Bryologist* **85:** 307–311.
Steere, W. C. 1940: Tortula in North America North of Mexico. *Bryologist* **43:** 12–23, 45–56, 76–86, 98–109.
Steere, W. C. 1948: Contribution to the bryogeography of Ecuador I. A review of the species of Musci Previously Reported. *Bryologist* **51:** 65–167.
Steere, W. C. 1975: Mosses and Hepatics from the Thule District, Northwest Greenland. *Amer. Midland Naturalist* **94:** 326–347.
Steere, W. C. 1977: Bryophytes from Great Lake and Coppermine, Northwest Territories, Canada. *J. Hattori Bot. Lab.* **42:** 425–465.
Steere, W. C., Scotter, G. W., Holmen, K. 1977: Bryophytes of Nahanni National Park and vicinity, Northwest Territories, Canada. *Can. J. Bot.* **55:** 1741–1767.
Stefureac, Tr. I., Mihai, Gh., Pascal, P. Barabas, V. 1973: Conspectul Briofitelor din Moldova. *Stud. Communic.* **6:** 129–258.
Stefureac, Tr. I., Kovács, A. 1981: Contrbuţii Florei Briologice din Muntii Bodoc (Jud. Covasna). *Stud. cerc. Biol., Ser. Biol. Veget.* **33:** 115–122.
Stefureac, Tr. I., Pascal, P. 1981: Conspectul Briofitelor din Bucovina. *Stud. Comunic. Ocrot. Nat.*, 471–544.
Størmer, P. 1963: Iranian plants collected by Per Wendelbo in 1959. VI. Mosses (Musci). Norwegian Universities Press, Bergen, Oslo, 36 pp.
Swann, E. L. 1982: Norfolk bryophytes today. *J. Bryol.* **12,** 77–112.
Swinscow, T. D. V. 1959: A bryophyte flora of Hertfordshire. *Trans. Brit. Bryol. Soc.* **3:** 509–557.
Szafran, B. 1957: *Mchy (Musci)* Tom. 1. Panstwowe Wyd. Naukowe, Warszawa, 449 pp.
Szmajda, P. 1979: Bryoflora Gór Stolowych i jej charakterystyka geobotaniczna. *Pozn. Tow. Przyj. Nauk. Wydz. Mat. Przyrod., Prace Komisji Biol.* **52:** 1–80.
Thornburgh, K. R., Sharp, A. J. 1975: A preliminary list of mosses collected on tree branches in Mexico. *Bull. Soc. Bot. Mexico* **35:** 51–58.
Townsend, C. C. 1977: Bryophytes from some Greek Islands. *Rev. Bryol. Lichénol.* **43:** 389–396.
Townsend, C. C. 1978: Notes on mosses from Ceylon and India, 1–5. *J. Bryol.* 10: 125–137.
Tuomikoski, R., Koponen, T., Ahti, T. 1973: The mosses of the Island of Newfoundland. *Ann. Bot. Fennici* **10:** 217–264.
Urbanek, H. 1966: Forest associations of the province of Lódz with special reference to Bryophyta. Part IV. A survey of the bryophytes occurring in forest associations. *Fragm. Flor. Geobot.* **12:** 151–178.

Vajda, L. 1959: Moose aus Griechenland. *Ann. Hist.-Nat. Mus. Nat. Hung.* **51:** 197–199.
Vanden Berghen, C. 1963: Quelques Bryophytes des Grands Causses septentrionaux (Aveyron et Lozère). *Rev. Bryol. Lichénol.* **32:** 56–64.
Vitt, D. H. 1976: Mosses new to the Yukon from Ogilvie Mountains. *Bryologist* **79:** 501–506.
Vitt, D. H. Koponen, T. 1976: Mosses of the Grande Cache Region of Alberta, Canada. *Lindbergia* **3:** 277–286.
Vitt, D. H., Horton, D. G. 1979: Mosses of the Nahanni and Liard ranges area, southwestern Northwest Territories. *Canad. J. Bot.* **57:** 269–283.
Vjunova, G. V. 1980: Materies ad Examinationem Bryoflore regionis Leningradiensis. *Nov. Syst. Plant. non. Vasc.* **17:** 216–230.
Wade, A. E. 1949: The bryophytes of Carmantshire. II. *Musci. Trans. Brit. Bryol. Soc.* **1:** 172–180.
Warburg, E. F., Crundwell, A. C. 1959: Tortula virescens (De Not.) De Not. new to the British Isles. *Trans. Brit. Bryol. Soc.* **3:** 568–570.
Warburg, E F. 1963–1966: New vice-county records and amendements to the Census Catalogue. *Trans. Brit. Bryol. Soc.* **4:** 492–504, 722–737, 859–874, **5:** 189–206.
Warnstorf, von C. 1911: Verzeichnis der von M. Fleischner 1908. während der Monate April und Mai Südfrankreich und Spanien beobachteten Laub- Leber- und Torfmoose. *Hedwigia* **50:** 189–203.
van der Wijk, R., Margadant, W. D. 1947: Voorlopige nieuwe naamlijst der Nederlandse Bryophyta. *Buxbaumia* **4:** 49–60.
van der Wijk, R., Margedant, W. D. 1960: Verslag van de excursie Naar Eernewonde, 11 Septemper 1960. *Buxbaumia* **14:** 39–44.
Woronoff, G. 1930: Nouvelles contributions à la flore bryologique de la Caucasie. *Rev. Bryol.* **57:** 105–122.
van Zanten, B. O., During, H. J. 1974: Contribution to the mossflora of the départements Pyrénées-Orientales and Aude. *Rev. Bryol. Lichénol.* **40:** 203–217.
Zsolt, J. 1943: A Szent-Endrei Sziget növénytakarója. *Index Horti Bot. Univ. Bud.* **6:** 1–19.
Zuttere, Ph. de, Schumacker, R. 1984: Bryophytes nouvelles, méconnues, rares, menacées ou disparues de Belgique. Ministere de la Region wallone. *Inspection générale de l'Environment et des Forêts. Service de la Conservation de la Nature*, **13:** 160 pp.
Абрамова, А. Л. Савич-Любицкая, П. И., Смирнова, З. Н. 1961: Определитель литостебелных мхов Арктики СССР. Издательство Академии Наук СССР, Москва, Ленинград-714 pp.
Абрамова, А. Л. Абрамов, И. И. 1983: Конспект флоры мхов Монгольской Народной Республики (Биологические ресурсы и природные условия Монгольской Народной Республики, Том 17.). Наука, Ленинград, 221 pp.
Бардунов, Л. В 1974: Листостебельные мхи Алтая и Саян. Издательство «Наука», Сибирское Отделение, Новосибирск, 168 pp.
Зеров, Д. К., Партика, Л. Я. 1975: Мохоподібні Українських Карпат. Издательство «Наукова Думка», Киев, 230 pp.
Мельничук, В. М. 1970: Определитель лиственных мхов средней полосы и юга европейской части СССР. Издательство «Наукова Думка», Киев, 442 pp.

EXSICCATAE

Brioteca Hispanica 1970, 1971.
Steere, W. C., Holmen, K. A., Mogensen, G. S. 1976: Bryophyta Arctica Exsiccata. Fasciculus II. (51–100). New York Botanical Garden.

Acta Botanica Hungarica 33 (3—4), pp. 279—294 (1987)

ECOLOGY, CENOLOGY, AND DISTRIBUTION OF THE GIANT PUFF-BALL *(LANGERMANNIA GIGANTEA* [BATSCH EX PERS.] ROSTK.) IN HUNGARY

I. Rimóczi

UNIVERSITY OF HORTICULTURE AND NUTRITION INDUSTRY, BUDAPEST

(Received: 10, October 1986)

The habitats, ecology and phytosociology of the giant puff-ball *(Langermannia gigantea)* and its chorological distribution in Hungary is studied and discussed.

Introduction

The habitats of giant puff-ball have been intensively studied to reveal the ecological and cenological characteristics of this fungus. Without their knowledge, this species can hardly be cultivated. Soil samples taken from below the basidiocarp and further away from the habitat were analyzed to find the optimum soil requirements of this fungus (Rimóczi 1985a, 1985b). Microclimate data recorded before the appearance of this fungus and during the growth of its basidiocarp yielded information on the temperature, precipitation and air humidity optima of giant puff-ball.

Considering preliminary data on the distribution and cenological relationships of this species (Rimóczi 1981, 1984), the main survey had the following objectives:

1. To examine the frequency of *Langermannia gigantea* habitats in the floristic units and vegetation zones of Hungary.
2. To evaluate cenological relevés for information on the possible cultivation of giant puff-ball. Aspects of this evaluation are: qualitative and quantitative characteristics of flowering plants, AD values for each level, life form, and frequency.
3. Synecological characterization of the most common species in the habitat of giant puff-ball, and the comparison of conclusions thus obtained with the results of ecological studies.
4. Cenosystematic identification of associations (community types) found in the habitat of giant puff-ball, to establish its sociability.
5. Characterization of habitats found in ecotopes influenced by primary, secondary and regular human impact.
6. To find the correct place of giant puff-ball among the native fungi of Hungary, and to evaluate its apophyton character, as far as cultivation is concerned.

Literature review

The assemblage of species of well-known ecological requirements, which occurs very frequently in the habitat of giant puff-ball, provides a reliable basis for estimating the characteristics of the fungus. This has been utilized by several researchers in Hungary and elsewhere for characterizing fungus species and communities, and even for the fine delimitation of plant communities.

MOSER (1949a) examined the fungi appearing on burnt spots after forest fires. The occurrence of several species (*Lyophyllum atratum* = *Tephrocybe atrata*, *Geopyxis carbonaria*, etc. and the *Morchella* genus) was in close connection with the succession of the recovering vegetation (MOSER 1949b). It is not surprising that many nitrophilous species showed up after forest fire (e.g. *Galium mollugo*, *Urtica urens*, and *Epilobium angustifolium*).

KREISEL (1957) studied the fungus flora of the Darss peninsula in the Mecklenburg area. Communities with which given fungus species were associated (e.g. *Pineto-Empetretum nigri*, *Armerietum maritimae*, *Molinietum coeruleae*, etc.) were identified. He reported that during the study the *Corynephoretalia* communities yielded high fungus phytomass thanks to heavy rains. According to their occurrence in plant communities, 359 fungus species were characterized. Seventeen species of puff-ball were included but *Langermannia gigantea* was an exception.

ŠMARDA (1972) examined fungus assemblages of various communities (*Potentillo-Quercetum pannonicum*, *Querceto-Carpinetum medio-europaeum*) based on 10–28 relevés. Several species were grouped according to their cenosystematic type (e.g. *Lactarius azonites* is querceticolous (= *Quercetalia*) species, *Lactarius acris* is fageticolous (= *Fagetalia*) species).

BENKERT (1976) made phytosociological relevés in the habitat of *Geoglossum* and *Trichoglossum* (Geoglossaceae, Helotiales). The flowering plants are listed in cenosystematic groups together with the cover values. Character species repeatedly and frequently co-occurring with these fungi receive emphasis. Since these species grow in grasslands, the high proportion of *Festuco-Bromea* and *Molinio-Arrhenatherea* species is not unexpected.

BENKERT (1978) also used relevés for characterizing the occurrences of *Marasmius capillipes* and *Amanita friabilis*. The AD values of species were given for each level.

In a survey of the production of fungi in northern Westphalia, BIRKEN (1976) made relevés with cover scores for each species. Then, the fungus production of certain communities (*Querceto roboris-Betuletum molinietosum*, *Betuletum pubescentis*, etc.) was compared and the association of fungus species with those communities was revealed.

UBRIZSY (1957) performed cenological investigations using 100 m² plots in several parts and vegetational zones of Hungary. Percentage cover data for each level were recorded. Continuous sampling of plant assemblages was used to determine the constant and dominant fungi of each community. Ten common puff-ball species occurred in his relevés (e.g. *Bovista plumbea*, *Calvatia saccata*, and *Lycoperdon perlatum*, etc.).

BOHUS and BABOS (1960) revealed actual relationships between fungi and co-occurring plants in relevés taken from different forest communities. For example, the mycorrhiza — host plant relationship of *Rosites caperata* and *Vaccinium myrtillus*, as supposed by LEISCHNEB —SISKA (1939), seems doubtful under the ecological conditions of Hungary, since this fungus was abundant in *Luzulo-Quercetum* communities completely free from *Vaccinium myrtillus*. Of the nearly 300 species listed, 10 were puff-balls, representing nine genera (including rare ones such as *Rhizopogon* and *Gautieria*).

BABOS (1982) lists the mushroom species found in the Hortobágy National Park, with reference to the plant community type in which each species was collected. The association of *Agaricus* species with plant community types is described in detail. Similar summarization for the mushrooms of Csévharaszt Nature Reserve and the Bugac Biosphere Reserve, Kiskunság National Park, is given in KONECSNI ((1974). No mention of *Langermannia gigantea* is made in these two papers, however.

There are very few papers reporting on the cenological status of *Langermannia gigantea*. Only KREISEL (1962) and RUNGE (1976) published cenological data exclusively on this species. Other authors give a short habitat description, mentioning a few co-occurring plants at most for example, RUNCK (1973) found 39 specimens under *Salix*, *Ulmus* and *Robinia pseudoacacia* in an area formerly covered by marshes.

Sous-Dorn (1979) collected *Langermannia gigantea* in a *Populus nigra* stand in which the shrub layer was 90% *Sambucus nigra* and 10% *Alnus glutinosa*, and the herb layer was 100% *Urtica dioica*. The same author collected this species under *Sambucus nigra* in a *Picea excelsa* stand, in which the herb layer was dominated by *Urtica dioica* and *Glechoma hedereacea*.

Kreisel (1962) prepared a distribution map of *Langermannia gigantea* in the GDR. Runge (1971, 1976) published the map of known records of this species in Westphalia. Gross et al. (1980) mapped the distribution of this species in FRG and West Berlin, using the grid system recommended for the European flora mapping project.

Kreisel (1962) listed alliances in which *Langermannia gigantea* occurs in GDR: *Chenopodietalia*, *Arrhenatheretalia*, and *Fraxino-Carpinion*. The latter cenosystematic taxon suggested by Tüxen corresponds in Hungary to the *Carpinion betuli* Soó in the *Fagetalia* order. Within these higher units, no information on associations was presented.

Runge (1976) is the only author who published detailed relevés from two habitats. Both of them are in the southern plain of Westphalia, on sand, in *Querco roboris-Betuletum* and *Populetum canadensis* "*cultum*", respectively.

The giant puff-ball, as a member of the mycoflora of Hungary, was first mentioned by Clusius in his detailed account on the Hungarian mushroom flora (Terpó et al. 1984).

Istvánffi (1899), Hollós (1903), and Moesz (1942) mentioned only localities without explicit description of the habitats. Their data originate mostly from cultivated lands such as vineyards, gardens, parks, edges of plough-lands, pig-farms, but they report some occurrences also from oakwoods and beechwoods. Szemere (1968) reports on two *Langermannia gigantea* occurrences in the Bakony Mountains, without describing the habitats.

Konecsni (1964), in his ecological and cenological studies around Gyömrő, found specimens of giant puff-ball in a pure *Robinia* stand in july. In september, he also observed this species in a locust tree stand near Nyíregyháza.

Takács and Siller (1980) present a sketchy cenological description on a Langermannia habitat ("Ősbükkös" near Szilvásvárad, Bükk National Park) by listing some more important character species. Since the giant puff-ball is said to live at the edge of "Ősbükkös", it is difficult to judge whether the published cenological data set is relevant to the immediate vicinity of the fungus.

Methods

The studies were always restricted to sites in which the basidiocarps of giant puff-ball were fresh white or mature and brown, and intact. The observations were mostly made in the autumn aspect. On the appearance of basidiocarps I was informed by students of mycological courses and the members of the Hungarian Mycological Society.

In the habitat of giant puff-ball, cenological relevés of 10×10 m^2 area were taken around the basidiocarp. All plant species found were recorded and the abundance-dominance values were determined according to the Braun-Blanquet scale for the tree, shrub and herb layers, and life form spectra were also determined. The constancy values of most common species in each layer were also calculated.

The synecological indicator values of these species were determined according to Soó (1980) and Ellenberg (1974), whereas their coenosystematic characterization follows Soó (1980). The nomenclature of species and plant communities follows Soó (1980).

The localities are shown on the vegetation map of Hungary according to the serial numbers of my notebook. The specimens collected are deposited in the herbarium of the University of Horticulture and Nutrition Industry.

Colour photographs were taken on almost all habitats I examined. The type of culture effects, the number of basidiocarps, and information on the age and former production of the given locality were also recorded. The degree of culture effects is expressed by the hemerobia scale, proposed by Jalas (1955) and Sukopp (1969) and re-interpreted by Terpó and Bálint (1983).

Since only one relevé was taken in each habitat, only the communities of primary ecotopes were unequivocally identified. In most habitats fragments of communities, degraded versions and plant assemblages of transitional or secondary character were found, so the single relevé taken is insufficient for a correct syntaxonomic identification. Therefore, only estimated community types were recorded in these cases.

Results and discussion

Cenological investigations were performed in 54 habitats (localities) of giant puff-ball. Documentation (collected specimen, photograph) is available from further 29 localities where no field studies were made. The herbarium of the Natural History Museum, Budapest, has

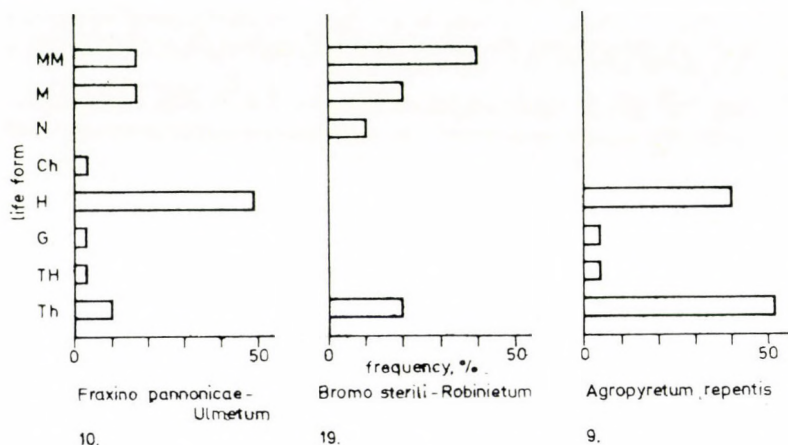



Fig. 1. Life-form spectra of co-occurring plants in three different habitats of *Langermannia gigantea*. Numbers below the names of communities refer to relevés (see Table 2)

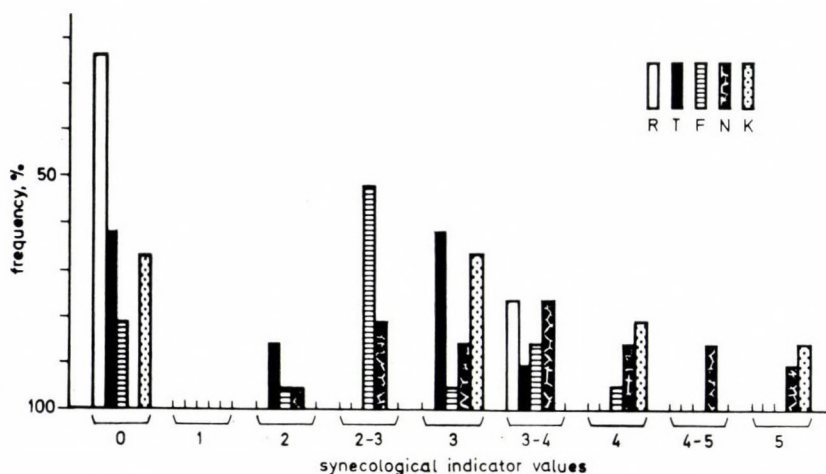



Fig. 2. The distribution of synecological indicator values of most common co-occurring plants in the habitats of *Langermannia gigantea* for explanation of abbreviations (see Table 1)

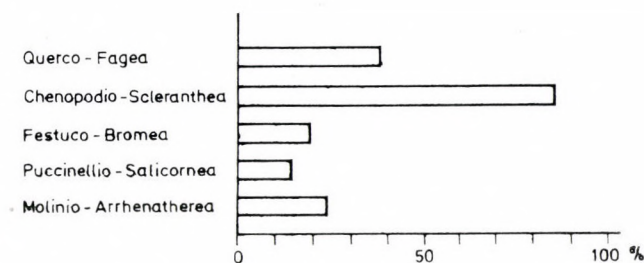



Fig. 3. The cenosystematic distribution of most common co-occurring plants in the habitats of *Langermannia gigantea*

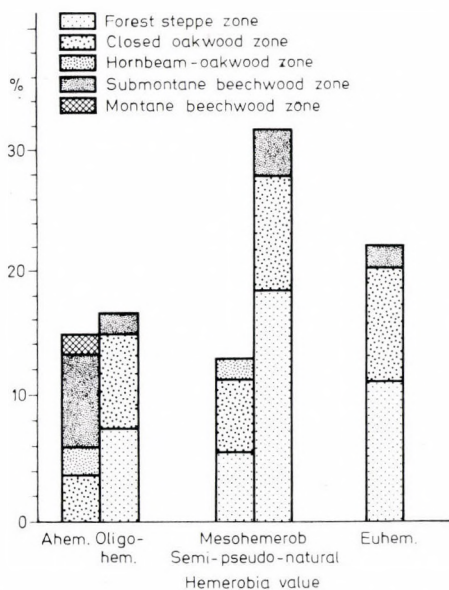



Fig. 4. The percentage distribution of habitats from various vegetation zones according to hemerobia types

prepared specimens from 11 localities. The Fungus Mapping Committee registered 218 localities until the end of 1985, without any documentation. Based on these data, and primarily on my own collections, I could draw conclusions regarding the distribution of *Langermannia gigantea* in Hungary. All localities are shown on the climazonal vegetation map of Hungary made by Borhidi (1961) (see Fig. 5).

Of the life form spectra of different habitats, only three are illustrated by the diagrams of Fig. 1; they exemplify different types.

The more or less common species were selected and listed in Table 1. according to their constancy in each layer, together with synecological indicator values and anatomical characteristics. The distribution of synecological indices for the most common species is shown in Fig. 2, whereas their cenosystematic distribution is given in Fig. 3. The classification of loca-

The climazonal vegetation of Hungary (Borhidi (1961)

Legend :

- Lowland forest steppe
- Hillside forest steppe and tartar maple-oakwood
- Closed oakwood zone
- Hornbeam-oakwood zone
- Submontane beechwood zone
- Montane beechwood zone

habitat

- ▲ Ahemerob or oligohemerob
- Mesohemerob
- Euhemerob
- △ Not examined in the field
- 49 Relevé N°

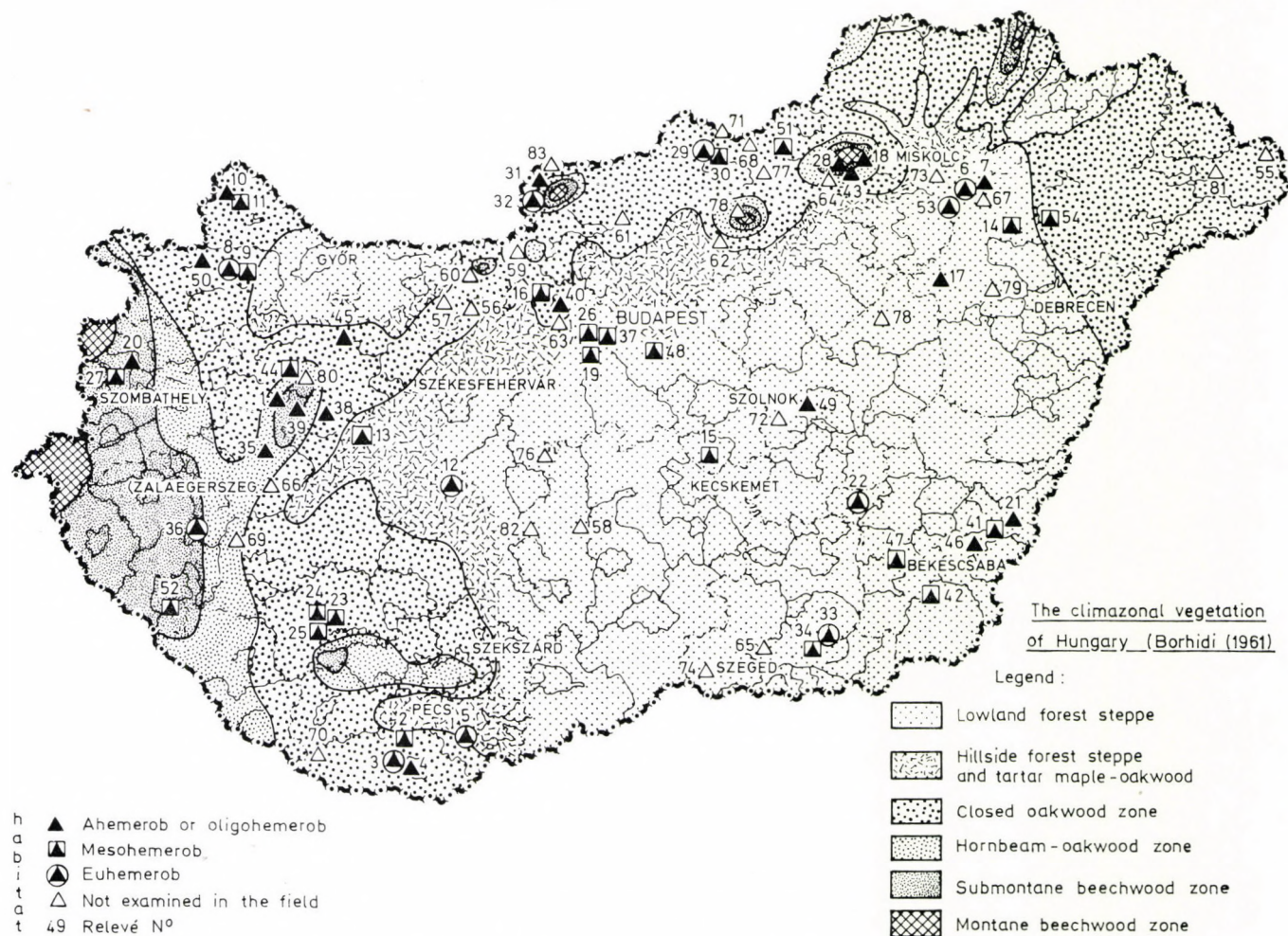



Fig. 5. Langermannia gigantea occurrences on the climazonal vegetation map of Hungary

Table 1

The classification of subconstant, accessory, and subaccessory species of Langermannia gigantea habitats according to layers, synecological and antomical properties

Constant	Subconstant	Accessory	Subaccessory	species	Synecological					Anatomical
					R	T	F	N	K	
					indices					
		Robinia pseudo-acecia			0	3	2	3–4	4	m
			Acer campestre		3–4	3–4	2–3	2–3	4	m
		Sambucus nigra			0	3	0	4–5	3	hg–m
			Clematis vitalba		3–4	3–4	3	3–4	3	m
			Crataegus monogyna		3–4	3	2–3	2	3	m–sk
			Rubus caesius		0	3	3–5	5	3	m
	Urtica dioica				0	0	3–4	4–5	X	hg–m
		Geum urbanum			0	3	2–3	3–4	5	m–hg
		Galium aparine			0	2	3–4	4–5	3	m–hg
		Ballota nigra			0	2	0	4	5	m
		Taraxacum officinale			0	0	2–3	2–3	X	hg–m
			Agrimonia eupatoria		3–4	3	2–3	3	4	m
			Glechoma hirsuta		0	0	2–3	2–3	3	m
			Arctium lappa		3–4	3	2–4	5	4	m
			Artemisia vulgaris		0	2	2–3	3–4	X	m–sk
			Stellaria media		0	0	2–3	3–4	X	hg
			Chenopodium album		0	0	0	4	X	m–hg
			Fallopia convolvulus		0	3	0	3	X	m–hg
			Agropyron repens		0	0	2–3	4	7	m–sk
			Agrostis stolonifera		0	0	3–4	2–3	X	m–he
			Dactylis glomerata		0	0	2–3	3	3	m

lities according to the vegetation zone and ecotope type, i.e. based on the hemerobia scale, is in Table 2 and is illustrated by Fig. 4.

Langermannia gigantea is present in all vegetation zones of Hungary (Fig. 5). Reflecting the proportion of areas of different vegetation zones, the highest number of occurrences, 23, fall within the forest steppe zone. Within this zone there is no difference between plains and mountainous areas.

The giant puff-ball has similar frequency in the zone of closed oakwoods this species was collected even in hornbeam-oakwoods and submontane beechwoods. One of the 54 localities falls to the zone of montane beechwoods; its elevation is about 800 m. This suggests that *Langermannia gigantea* is mainly restricted to the plains and mountains of medium elevation. In the GDR, most localities are reported from the plains as well (Kreisel 1962). The situation is similar in Westphalia (Runge 1976). Nevertheless, these authors report on records from mountainous areas, too. It is not surprising that to the northwest the planar-colline character of this fungus becomes predominant; this has been reported on other species (Gross *et al.* 1980).

According to the data collected for the Fungus Mapping Committee (Konecsni, unpubl.), there are records from every county of Hungary. This fact, and my data support that *Langermannia gigantea* is present in every flora district; no area can be selected as being much more productive than the others.

Clearly, edaphic factors, rather than climazonal effects determine primarily the distribution of giant puff-ball, at least in Hungary, as the vertical distributional limit (1000 m, GROSS et al. 1980) is irrelevant.

As a result of the widespread occurrence of *Langermannia gigantea*, there are many (355) plant species in the 54 relevés. They belong to 45 orders and 70 families. Dominant taxa are: Compositace (47 species), Gramineae (30 species), Rosaceae (29 species), and Fabaceae (22 species). Forty species were recorded from the tree level, 34 from the shrub layer and 281 from the herb layer. The number of species may be as much as 48–51 per quadrat in the primary ecotopes of the mountains, whereas in some cultivated areas this number is sometimes lower than 10.

In summary, 21% of the species occur in the tree and shrub layer. If we examine the levels in the habitats, it becomes obvious that the giant puff-ball is a shade-plant. It is especially true for the initial, sensitive stage of its growth, when its size is about 9–12 cm, and a relatively dense herb layer is sufficient enough to provide the shade. Over this critical period, the fungus does not require shade any longer and may reach extremely large size even on sunny, southern slopes (although it is not too common; these occurrences are the most striking, anyway).

Only 11% of the giant puff-ball habitats lack tree and shrub layers; but in these places herb layer is tall and well-developed (relevés 6, 8, 9, 25, 26 and 34). The same is true for four localities (3, 33, 36 and 40) where only shrub layer is found over the herbs. In places with sparse herb layer (cover less than 75%), the upper and lower tree levels are well-developed, and the shrubs form an almost impenetrable bush. These layers provide the shade necessary for the early development of the basidiocarp. In most habitats (62%), the tree and shrub levels are well-developed, the cover of herbs is complete so that basidiocarps start to develop under diffused light.

The basically shade-loving character of giant puff-ball, although not equally important in the developmental stages, has to be considered when this species is cultivated. The relationship between light/shade ratio and production was pointed out by BIRKEN (1976) as well.

It follows from the above discussion that the life form spectra of habitats strongly differ from one another. Three extreme cases are illustrated in Fig. 1.

The higher plants growing in a habitat determine primarily the type of fungus potentially occurring. Thus, the floristic composition in the habitat of giant puff-ball may be indicative of the nutritional properties of this fungus. Most genera of the Gasteromycetes class are saprobionts, although there are some genera with mycorrhiza (e.g. *Phallus*). Thus, in case of *Langermannia gigantea* a facultative mycorrhiza relationship is also possible or necessary for the development of the basidiocarp. Habitats without trees and shrubs, such as No. 9 in Fig. 1, exclude the possibility for symbiosis with woody plants. Where the herb layer is composed of two therophytes (*Bromus sterilis* and *Chenopodium album*) only, whose vegetative period in that community (*Bromo sterili-Robinietum*) is extremely short, symbiosis with herbs will be impossible.

These cenological data suggest that *Langermannia gigantea* is a saprobiont, which is an important property as far as cultivation of this species is concerned.

Many plant species observed in the habitat of giant puff-ball are restricted to one or a few relevés. Although these species may indicate very important characteristics of the habitat (e.g. *Helleborus odorus* in the Sopianicum flora district, *Lunaria rediviva* at higher elevations in the Transdanubian mountains), essential properties of the fungus can be deducted only from species that are present in most relevés. For this reason, 21 species from the 355 found in the 54 relevés were selected according to frequency (Table 1). None of them is constant (i.e. present in more than 80% of the relevés). Urtica dioica is subconstant, it is present in 23 relevés (61%) usually with high AD values. Accessory species in the tree level is *Robinia*

pseudoacacia, in the shrub layer *Sambucus nigra*, whereas in the herb layer *Geum urbanum*, *Galium aparine*, *Ballota nigra* and *Taraxacum officinale*. These species are present in 40–59% of the relevés, sometimes with high AD values. There are 10 subaccessory species in the herb layer, 3 in the shrub layer and one in the tree layer.

Conclusions can be made on *Langermannia gigantea* based on the synecological indicator values (soil reaction — R; temperature — T; soil humidity — F; nitrogen requirement — N, cf. Soó 1980), continentality (K) and anatomical properties (Ellenbebg 1974) of the 21 common species (Fig. 2). There is example in the literature that synecological indices of mushrooms are determined similarly to those of higher plants. Krieglsteiner (1981, 1982) published synecological indicator values for 170 fungus species, using data of mapping projects and other observations. In addition to soil reaction (R), temperature (W), soil humidity (F) and nitrogen requirement (N), he included the life style of species (L), the type of habitat (S), the most characteristic vertical position of the habitat (H) and its area (A).

Bohus and Babos (1967) determined synecological indicator values of soil reaction (R) for many fungi, including 3 puff-balls, based on coenological investigations and soil reaction measurements in acidophilous forests of Hungary (Bohus 1984). *Langermannia gigantea* is not mentioned in these papers.

As to soil reaction, most of the common higher plants in the habitats of giant puff-ball are widely indifferent, some occurring also on neutral and weakly basic soils. According to detailed measurements, however, *Langermannia gigantea* is not so widely indifferent but rather an acido-subacidophilous (pH 5.7–5.9) species (Rimóczi 1985a). The frequency of indifferent species is not contradictory, since these plants tolerate this weakly acidic soil as well.

Regarding temperature requirements, most co-occurring plants are widely indifferent or, in the same proportion, indifferent, with moderate rather than weakly termophilous character. This statement is completely valid for *Langermannia gigantea*, since it grows from the end of May till the end of October. Although the 10–12 °C difference between the mean temperature may slow down the growth of this fungus by 60%, a 2–3 cm/day increase of height may still be achieved. That is why the giant puff-ball may survive in the more elevated parts of the mountains of Hungary.

Langermannia gigantea is mesophilous rather than indifferent to soil humidity. This conclusion follows from the indicator values of co-occurring plants and is confirmed by microclimate measurements (Rimóczi 1987). The shade-plant character of giant puff-ball is not conflicting with this requirement.

The very high nitrogen demand of giant puff-ball is confirmed by the synecological indicator values of the co-occurring plants. Some of them are mesophilous for N, but the majority are nitrophilous or pernitrophilous. Compared with two relevés of Runge (1976), *Urtica dioica* is also dominant (in my relevés it is subconstant) and *Sambucus nigra*, *Stellaria media*, *Galium aparine*, and *Taraxacum officinale* are all present; these species are significant constituents of the communities in *Langermannia* habitats. Nevertheless, the giant puff-ball and *Urtica dioica* co-occur frequently due simply to their common nitrophilous character; symbiosis is unlikely since Urtica dioica is absent from 21 relevés (in these localities other nitrophilous species indicate the high nitrogen content of the soil: *Galium aparine*, *Arctium lappa*, and *Chaerophyllum bulbosum*, etc.).

On the continentality scale of Ellenbebg (1974), the co-occurring higher plants are partly widely indifferent and partly central European with subcontinental character. This intermediate status holds also for *Langermannia gigantea*, as it grows in habitats with strong temperature and air humidity fluctuations, in steppe patches of rock slopes with different exposure and even in fescue grass steppes in the plains, although these are not its most common habitat types. The frequent appearance of *Langermannia* in July and August, after the pro-

ductivity peak of early summer and before another peak in autumn, also refers to this fact. At this time of the year the production of many mushrooms is the minimum (BOHUS 1952, IMREH and BOHUS 1969).

It is interesting that according to Ellenberg's classification based on anatomical characters, the co-occurring plants are of the mezomorph type, with hygromorph character (fine, fragile structure, preference for shade or half shade). This indicates quite well the habitat requirement of *Langermannia gigantea.*

Based on the synecological indicator values of the most common species found in the habitat of the giant puff-ball, it is possible to draw conclusions on the synecological values of this fungus. These values on Soó's (1980) scale are: R = 2–3 (0) (according to measurements rather than considering the co-occurring plants); T = 0 (2–3); F = 3 (0); N = 4–5 (analytical studies reject the possibility of lower categories); and K = 3–5 (0). Continentality is given on ELLENBERG's (1974) scale.

Taking the 21 species as 100%, the percentage of most common species in the coenosystematic divisions is as follows (Fig. 3): 85.7% *Chenopodio-Scleranthea* species; 38.0% *Querco-Fagea* species; 23.8% *Molinio-Arrhenatherea* species, 19.0% *Festuco-Bromea* species, and 14.2% *Puccinellio-Salicornea* species. The common species in RUNGE's (1976) relevés also belong to these divisions, but there are constant species from *Nardo-Callunetea* (*Agrostis capillaris*) and *Pino-Quercetalia* (*Holcus lanatus*) as well.

Concluding the above remarks, *Langermannia gigantea* may appear in all of the five divisions, but it is especially characteristic of *Chenopodio-Scleranthea* and *Querco-Fagea.*

However, if we consider all community types found (or supposed) to be in each locality, the picture will be somewhat different from that outlined above.

Regarding the percentages of plant communities identified or supposed in the quadrats based on all the species present, the alliances of *Querco-Fagea* (*Fagetalia, Quercetalia pubescentis, Orno-Quercetalia*) stand for 37%, followed by the *Chenopodio-Scleranthea* communities (27.7%), *Molinio-Arrhenatherea* (11.1%), *Festuco-Bromea* (5.5%). In communities belonging to *Puccinellio-Salicornea* there was no giant puff-ball found.

The difference from the classification using only the dominant species arises from the fact that in nine localities *Bromo sterili-Robinietum* and in one locality *Populus canadensis* "cultum" were found. These are considered as being "silvae cultae" in Soó's (1980) syntaxonomical system, sharply separated from the other divisions. In these ten localities no plant species were found which could have been used to reconstruct the original vegetation type. Therefore, the *Chenopodio-Scleranthea* (e.g. *Robinia pseudoacacia*) and *Puccinellio-Salicornea* (e.g. *Agropyron repens*) species so characteristic of "cultured" forests had to be excluded from the syntaxonomic analysis.

At last, I do not need to modify the statement that *Langermannia gigantea* is a character species of *Chenopodio-Scleranthea* and *Querco-Fagea.* In addition, however, it must be noted that this fungus is more common in *Querco-Fagea* and its derivatives, degraded types and fragments, and also in plantations and culture forests.

The cenological identification of habitats in the primary ecotopes is sometimes difficult since *Langermannia gigantea* is found in transitional or disturbed areas in which the dominant species of communities are replaced by indifferent plants of wide ecological amplitude.

Again, it is to be noted that the distribution of *Langermannia gigantea* is mostly affected by edaphic factors rather than phytosociological effects.

The commonness of this fungus in secondary ecosystems and ecotopes under regular human impact follows from the fact that in the habitat of *Langermannia gigantea* plants of wide ecological tolerance, or indifferent and nitrophilous species dominate, such as some very common weeds (*Ballota nigra* and *Agropyron repens*).

Table 2

Classification of identified and reconstructed community types of Langermannia gigantea habitats according to climazonal vegetation zones and ecotope types (hemerobia values)

Zone	Primary ecotopes		Secondary ecotopes Mesohemerob		Ecotopes under regular human impact Euhemerob
	Ahemerob	Oligohemerob	semi-natural	pseudo-natural	
Mountain beechwood	28. *Tilio — Fraxinetum hungaricum, Poa nemoralis* fac.				
Submountain beechwood	1. *Mercuriali — Tilietum, Melica uniflora* fac. 18. *Mercuriali — Tilietum, Smyrnium perfoliatum* fac. 39. *Melitti — Fagetum hungaricum asperuletosum, Aegopodium podagraria* fac. 43. The same item as 39.	20. *Fraxino pannonicae — Ulmetum pannonicum, Fraxinus excelsior* consociation		27. *Filipendulo — Geranietum palustris, Phragmites australis* typ. (strongly degraded fragment). 52. *Populetum canadensis* "cultum", *Urtica dioica* typ.	36. *Alopecuretum pratensis* (strongly degraded, on its polluted part with dung water, *Sambucus nigra, Urtica dioica*)
Hornbeam oakwood	35. *Querco petraeae — Carpinetum pannonicum asperuletosum, Glechoma hirsuta* fac.		44. *Angelico — Cirsietum oleracei* (regenerating, abandoned orchard)		
Closed oakwood	4. *Tilio argenteae — Quercetum petraeae — cerris* 38. *Tilio — Fraxinetum hungaricum, Glechoma hirsuta* fac.	20. *Fraxino pannonicae — Ulmetum pannonicum quercetosum* 40. *Pulsatillo — Festucetum rupicolae* 45. *Querco petraeae — Carpinetum pannonicum* 50. *Fraxino pannonicae — Ulmetum pannonicum quercetosum*	16. *Lolietum perennis* (secondary mountain meadow with Lolium perennis dominating?) 30. *Quercetum petraeae — cerris Robinia pseudo-acacia* culture cons. (very weedy) 51. *Chaerophylletum bulbosi*	2. *Bromo sterili — Robinietum* 9. *Agropyretum repentis* 23. *Bromo sterili — Robinietum Galium aparine* typ. 24. *Bromo sterili — Robinietum Sambucus nigra* typ. 25. The same item as 27.	3. *Urtico dioicae — Conietum maculati* 8. The same item as 3. 29. *Lolio — Plantaginetum majoris* 31. *Sambucetum ebuli* 32. *Echinochloo — Setarietum portulacetosum*
Forest steppe		7. *Fraxino pannonicae — Ulmetum pannonicum populetosum* 17. *Fraxino pannonicae — Ulmetum pannonicum quercetosum* (partly degraded) 21. *Fraxino pannonicae — Ulmetum brachypodietsum* 49. The same item as 10.	13. *Aceri tatarico — Quercetum* (now wet *Robinia* plantation) 14. *Aceri tatarico — Quercetum* (now culture consociation of *Fraxinus pennsylvanica*) 15. *Convallario — Ligustro — Quercetum roboris, Urtica dioica* fac. (now rather *Robinietum*)	11. *Cleistogeno — Festucetum rupicolae* (strongly degraded) 19. The same item as 24. 26. *Agropyro — Convolvuletum arvensis* (with species from the neighbouring *Festucetum vaginatae danubiale* fragments) 34. *Agropyro — Convolvuletum arvensis* (with species from the neighbouring *Festucetum pseudovinae* fragments) 37. *Bromo sterili — Robinietum Bromus sterilis* typ. 41. *Convallario — Quercetum* (strongly degraded, now rather *Robinietum*) 47. The same item as 24. 48. *Bromo sterili — Robinietum, Chelidonium majus* typ. 54. *Bromo sterili — Robinietum, Stellaria media* typ.	5. *Arctio — Ballotetum nigrae, urticetosum dioicae* 6. *Arrhenatheretum elatioris* (secondary association) 12. *Hordeo murini — Chenopodietum albi* 22. *Digitario — Portulacetum* 33. *Digitario — Portulacetum* 46. *Agrostetum albae hungaricum* (edge of vineyard) 53. *Lolio — Plantaginetum majoris*

The community types of the 54 localities are summarized in Table 2 according to vegetation zones and hemerobia indices. Figure 4 demonstrates the percentage distribution of habitats representing a hemerobia value over the vegetation zones.

In the primary ecotope 17 communities contained *Langermannia gigantea*. Out of these, eight habitats are ahemerob (where the anthropogenic effects are negligible). None of them falls to the forest steppe zone, as expected, since undisturbed primary ecotopes are strongly reduced in area in this zone. Starting from the closed oakwoods, giant puff-ball is present in many associations up to the montane beechwood. Large specimens were found in several types of *Tilio-Fraxinetum* and *Mercuriali-Tilietum*. In the other 9 habitats of primary ecotopes, the anthropogenic effects are moderate, but clearly visible (oligohemerobia). Four habitats of this kind occurred in the forest steppe zone as various subassociations of *Fraxino pannonicae-Ulmetum*. Along the Tisza and Körös rivers and in the deeper and wetter parts of the Ohat-forest are found these habitats. The anthropogenic influences are shown by the establishment of alien tree species (*Juglans nigra*, *Celtis occidentalis*) and the occurrence of statophytes (e.g. *Solidago gigantea*).

In the closed oakwood zone, *Fraxino pannonicae-Ulmetum* is also the habitat of *Langermannia gigantea;* in addition this fungus is found in *Querco petraeae-Carpinetum* where some *Robinia pseudoacacia* individuals indicate the favourable edaphic conditions.

Most habitats of the giant puff-ball, 44% of the total, are mezohemerob, i.e. occur in secondary ecotopes. Here, anthropogenic effects were either formerly intensive and later disappeared or still existing in various forms (waste deposits, dung water infiltration, allelopathic effects of introduced species, etc.).

No data in the literature were found on the anthropogenic effects on the distribution and production of a single fungus species. I am aware of papers reporting on general effects of human activities only, e.g. fertilization (Bujakiewicz 1979), forest fire (Moser 1949, Bujakiewicz 1979). In these works very little information is presented on puff-ball, and *Langermannia gigantea* is not mentioned at all.

In a smaller part of habitats in secondary ecotopes, strong culture effects prevailed some decades ago: original communities were disturbed, fruit-trees and shrubs were planted (relevés 16, 44, and 51) or the foliage level was replaced (in *Querco petraeae-Carpinetum*, relevé 30). Elsewhere a culture consociation of *Aceri tatarico-Quercetum roboris* with *Robinia pseudoacacia* was developed (relevés 13 and 14). These habitats are of seminatural, mesohemerob character; in addition to the abundant nitrophilous weeds in the shrub and herb layers, the species of the original communities are also well-represented. Such habitats are found from the forest steppe to the hornbeam-oakwoods (here replacing the *Angelico-Cirsietum oleracei* community).

The pseudo-natural type of secondary ecotopes is richer in *Langermannia* habitats. Here, the original vegetation could hardly be reconstructed, since even in the herb layer no reference species are present. Most of them are various wet or semihumid types (*Urtica dioica*, *Galium aparine* types) of *Bromo sterili-Robinietum*, *Populetum canadensis* plantations, or strongly degraded grassy areas replacing the original *Festucetum pseudovinae* and *Festucetum vaginatae* communities. In these places intensive keeping of livestock influenced the vegetation, and sometimes livestock farms are still found in the nearest vicinity. Dung water and other waste material, e.g. pollution from mills, get into the area continuously or occassionally. The locust trees also enrich the soil in nitrogen and, at the same time, they add allelopathic compounds to the environment. These effects inhibit recolonization by the original plants of the area but do not disturb the life of giant puff-ball. Indeed the high N content of the soil is favourable for fungi. Thus, these habitats with locust trees and elder thickets, nettle understorey and wet, shady and nutrient-rich environment are the most acceptable for *Langermannia gigantea*. Such ecotopes are commonly formed in the zone of forest steppe, and also

occur in the closed oakwoods and even in the submontane zone (e.g. replacing *Filipendulo-Petasition*).

The study of habitats under regular human impact may give the most useful information on the cultivation of *Langermannia*. Within this ecotope, giant puff-ball occurs only in the euhemerob type; the polyhemerob and metahemerob types are not suitable for this fungus, even though in the polyhemerob type (such as a sawdust deposit) sometimes highly productive mycocenoses were observed (Babos 1981). In these habitats some species of puff-ball were also observed. In the euhemerob areas subspontaneous plants replace the original species; species poor weedy flora occurs among the cultivated plants in intensive plough lands, parks and gardens.

On the margins of intensive plough-lands, e.g. at cornfields (relevé 6), at the edge of a lucerne field (relevé 57) and beside manure heaps, giant puff-ball was also collected. In the weedy parts of parks in livestock farms and manors, due to regularly infiltrating dung water, *Urtico dioicae-Conietum maculati* (relevé 3), *Arctio-Ballotetum nigrae urticetosum dioicae* (relevé 15) and, in drier places, *Hordeo murini-Chenopodietum albi* (relevé 12) weed communities developed, in which *Langermannia* is very productive regularly.

In all gardens with the spontaneous occurrence of *Langermannia gigantea*, big quantities of various fertilizers were deposited in the previous 1–2 years. The fungus is absolutely insensitive in its production on the plant species cultivated in the garden. It grows in vineyards, as well as among strawberry or red currant plants. In turfed front gardens and in aster beds this fungus may reach equally large sizes. Shallow hoeing and the usual sprayings do not inhibit the fungus, except in the fruiting period.

In garden habitats the most common weed communities may be identified: *Lolio-Plantaginetum majoris* (relevés 29, 53), *Digitario-Portulacetum* (relevés 22, 23) and *Echinochloo-Setarietum portulacetosum* (relevé 32).

The *Langermannia gigantea* individuals living in cultivated lands are equally frequent in the zone of forest steppe and closed oakwoods, but their occurrence in more elevated zones is also likely. Thus, its future cultivation will not be affected by climazonal belts.

The giant puff-ball is now more common in the secondary ecotopes and in areas under regular human impact, especially in cultivated lands, than in natural habitats.

This fungus is a character species of *Querco-Fagea* and *Chenopodio-Scleranthea*, as our studies suggest. *Langermannia gigantea* grows in *Querco-Fagea* communities (especially *Fagetalia* within which in *Ulmion*, and also in *Aceri tatarico-Quercon* of *Quercetalia pubescentis*) in the primary ecotopes and seminatural habitats of secondary ecotopes. It occurs to a lesser extent in *Molinio-Arrhenatherea*; within this in degraded *Filipendulo-Cirsion* (*Molinietalia*) and in drying bog meadows (*Molinion*) and mountain meadows (*Arrhenatherion*). These are the natural habitats of *Langermannia gigantea* among the native species of Hungary.

A consequence of the wide ecological amplitude of this fungus and the edaphic conditions of its presence is that the anthropogenic effects on vegetation increased rather than decreased the suitable habitats. The degradation of original communities, the formation of seminatural ecotopes in secondary ecotopes, and then the complete destruction of the natural flora were followed by euhemerob ecotopes which represent favourable habitats for the giant puff-ball. *Langermannia gigantea* is mostly found in *Chenopodio-Scleranthea* (mainly *Sisymbrietalia*, such as *Convolvulo-Agropyrion*, or *Artemisietalia*, such as *Arction lappae*) weed communities.

Thus, the native fungus follows culture effects; the seminatural or completely anthropogenic environments are favourable for it. In these habitats, *Langermannia gigantea* may even be more common than in natural communities, i.e. this fungus is an apophyte.

According to the places in which this species became an apophyte, we may distinguish the following types: segetal apophyte (at plough lands), ruderal apophyte (along roadsides,

waste deposits and dung water drainage lines), grassland apop hyte (in anthropogenic meadows and pastures), and plantation apophyte (in locust tree and p oplar stands).

The large puff-ball colonies spontaneously establishi ng in these habitats, especially in the gardens, prove that the cultivation of this fungus is not an impossible task. In eleven gardens out of the 83 habitats, this has already b een a reality, and further systematic research will lead to an extensive or intensive cultivatio n of the giant puff-ball.

Summary

Cenological studies were performed in 54 habitats of *Langermannia gigantea*, in 10×10 m^2 quadrats around the basidiocarp. The relevés (355 species), the AD values of plants at each level, the life-form spectra, the synecological and cenosystematic characteristics, the plant communities identified in the field and the degree of culture effects (hemerobia values) allow for the following conclusions:

1. *Langermannia gigantea*, although not common, occurs in the whole area of Hungary. In the zone of forest steppe and closed oakwoods, this species is relatively more frequent, and also occurs in hornbeam-oakwoods, submontane and montane beechwoods. It is a species of plains and mountains of medium elevation. Its distribution is primarily influenced by edaphic factors; the climazonal factor is less substantial.

2. 355 species were recorded in 54 localities. Compositae, Gramineae and some other weed families dominate. The tree and shrub levels are well-developed; if they are absent (11% of localities) then the herb layer is dense and tall. In the early developmental stages, this fungus requires complete shade and later it remains shade-loving, although tolerates strong illumination. The life form spectra determined in its various habitats exclude the possibility of mycorrhiza relation of giant puff-ball with trees and perennial herbs.

3. There are no constant species in the localities examined; *Urtica dioica* is subconstant, *Robinia pseudoacacia*, *Sambucus nigra*, *Geum urbanum*, *Galium aparine*, *Ballota nigra* and *Taraxacum officinale* are accessory species. Fourteen subaccessoric species were recorded. The synecological indicator values of *Langermannia gigantea*, as deduced from those of co-occurring plants, are as follows: indifferent to soil reaction, although avoids basic soils (R = 2–3 (0)), indifferent to temperature, but not termophilous (T = 0 (2–3)), mesophilous to soil humidity (F = 3 (0)), strongly nitrophilous (N = 4–5), and continentality intermedier (K = 3–5 (0)). These figures are in accordance with pedological and microclimate measurements.

4. Based on the cenosystematic classification of most common co-occurring plants, and on the cenosystematic identification or reproduction of communities using complete relevés, *Langermannia gigantea* is a character species of *Querco-Fagea* and *Chenopodio-Scleranthea* and also common in "Silvae cultae", especially *Bromo sterili-Robinietum*.

5. The communities that are considered as primary ecotopes are found in most vegetation zones except the forest steppe belt. The fungus is most abundant in secondary ecotopes, in seminatural and especially pseudo-natural habitats in the forest steppe and closed oakwood zone. In the euhemerob type of ecotopes continuously influenced by human activity, on intensively cultivated agricultural fields, this fungus appears spontaneously.

An important conclusion of the above results is that the cultivation of this fungus in the future need not be restricted to specific vegetational zones.

6. As a character species of *Querco-Fagea* (and *Molinio-Arrhenatherea*), *Langermannia gigantea* belongs to the native mycoflora of Hungary. Due to human impact on vegetation, this fungus becomes characteristic of *Chenopodio-Scleranthea* communities which are found in mezohemerob and even euhemerob habitats. Then, as an apophytic species, the guarantee for its cultivation lies in the fact that *Langermannia gigantea* follows the extension of culture lands.

REFERENCES

Babos, M. 1981: Mycological examination of sawdust depots in Hungary. — *Studia Bot. Hung.*, **15:** 31–44.

Babos, M. 1982: Higher fungi of the Hortobágy. — *The Flora of the Hortobágy National Park*, p.: 63–89.

Benkert, D. 1976: Bemerkenswerte Ascomyceten der DDR. II. — *Mykol. Mitteilungsbl.*, **20**/3: 47–93.

Benkert, D. 1978: Bemerkenswerte Pilzfunde aus Brandenburg. III. — *Mykol. Mitteilungsbl.*, **22:** 2/3: 41–64.

Birken, S. 1976: Pilzfloristische Untersuchungen im nördlichen Westfalen — *Zeitschr. f. Pilzkunde*, **42:** 95–112.

Bohus, G. 1952: Növénytársulások, életfeltételek, a gombafajok száma és mennyisége a budaihegységi Hársbokor-hegyen és környékén. (Plant communities, life conditions, quantity and quality of mushroom species at the surroundings of the Hársbokor-hegy.) — *Ann. Hist.-Nat. Mus. Nat. Hung.*, **2:** 281–285.

Bohus, G. 1984: Studies on the pH requirement of soil-inhibiting mushrooms: the R-spectra of mushroom assemblages in deciduous forest communities. — *Acta Bot. Hung.*, **30:** 155–171.

Bohus, G., Babos, M. 1960: Coenology of terricolous macroscopic fungi of deciduous forests. — *Bot. Jb.*, **80:** 1–100.

Bohus, G., Babos, M. 1967: Mycocoenological investigation of acidophilous deciduous forests in Hungary. — *Bot. Jb.* **87:** 304–360.

Borhidi, A. 1961: Klimadiagramme und klimazonale Karte Ungarns. — *Ann. Univ. Sci. Budapest, Ser. Biol.* **4:** 21–50.

Bujakiewicz, A. 1979: A nagygombák szerepe és jelzőértéke a Babia Gora hegység erdőtársulásaiban. (The role and indicator value of the mushrooms in the forest communities of the Babia Gora Mountains.) — *Mikol. Közlem.* **2:** 75–88.

Ellenberg, H. 1974: Zeigerwerte der Gefäßpflanzen Mitteleuropas. — *Scripta Geobot.*, **9:** 1–97.

Gross, G., Runge, A., Winterhoff, W. 1980: Bauchpilze (Gasteromycetes s. l.) in der Bundesrepublik und Westberlin. — *Beih. z. Zeitschr. f. Mycol.* **2:** 1–220.

Hollós, L. 1903: *Magyarország Gasteromycetái* (The Gasteromycetes of Hungary). Budapest.

Imreh, L., Bohus, G. 1969: Studien zu den ökologischen Verhältnissen von *Agaricus maskae* Pilát. — *Schw. Z. F. Pilzk.*, **47:**/2: 17–25.

Istvánffi Gy. 1899: *A Magyar Ehető és Mérges Gombák Könyve.* (Manual of the Hungarian edible and poisonous mushrooms.) Budapest

Jalas, J. 1955: Hemerobe und hemerochore Pflanzenarten. Ein terminologischer Reformversuch. — *Acta. Soc. Fauna Flora Fenn.*, **72:**/11. p.: 1–15.

Konecsni, I. 1964: Gomba ökológiai és cönológiai vizsgálatok I. Adatok az akácerdőkben termő nagygomba fajokról. (Ecological and coenological studies on mushrooms. I. Macromycetes of the Robinia plantations.) — *OMMI Évkönyv*, **6:** 331–350.
Konecsni, I. 1974: Adatok a Csévharaszti Természetvédelmi Terület és ligeterdők gombáihoz. (Contributions to the mushroom-flora of the alluvial forests of the Csévharaszt Natural Conservation Area.). — *Abstracta Botanica*, **2:** 77–93.
Konecsni, I. 1984: A Kiskunsági Nemzeti Park bugaci bioszféra rezervátumának és környékének makrogombái. (Macromycetes of the Biosphere Reserve Bugac in the Kiskunság National Park and its surroundings.). — *Abstracta Botanica*, **8:** 57–72.
Kreisel, H. 1957: Die Pilzflora des Darss und ihre Stellung in der Gesamtvegetation. — *Feddes Rep., Beih.*, **137:** 110–183.
Kreisel, H. 1962: Die Lycoperdaceae der Deutschen Demokratischen Republik. — *Feddes Rep.*, **64:** 89–201.
Krieglsteiner, G. 1981: Verbreitung und Ökologie 150 ausgewählter Blätter- und Röhrenpilze in der Bundesrepublik Deutschland. (Mitteleuropa). — *Beih. z. Zeitschr. f. Mycol.* **3:** 1–267.
Krieglsteiner, 5. 1982: Verbreitung und Ökologie 200 ausgewählter Röhren-, Blätter-, Poren- und Rindenpilze in der Bundesrepublik Deutschland. (Mitteleuropa) — *Beih. z. Zeitschr. f. Mycol.* **4:** 1–270.
Leischer-Siska, E. 1939: Zur Soziologie und Ökologie der höheren Pilze. — *Beih. z. Bot. Zentr. Abt. B.*, **59:** 359–429.
Moesz, G. 1942: Budapest és Környékének Gombái (Die Pilze von Budapest und seiner Umgebung). Budapest.
Moser, M. 1949: Untersuchungen über den Einfluss von Waldbränden auf die Pilzvegetation I. — *Sydowia*, **3:** 336–383.
Moser, M. 1949b: Über das Massenauftreten von Formen der Gattung Morchella auf Waldbrandflächen. — *Sydowia*, **3:** 174–195.
Nehéz, Z. 1985: Termesztésélettani kísérletek Langermannia giganteával. (Production physiological experiments on Langermannia gigantea.) — *Mikol. Közlem.*, **1–2.** 61–68.
Rimóczi, I. 1981: Studies on the coenological and ecological relations of *Langermannia gigantea* in Hungary. — *VIII. Congress of European Mycologists.* Budapest, Abstracts.
Rimóczi, I. 1984: Records of *Langermannia gigantea* (Batsch ex Pers.) Rostk. in cultivated lands. — *16th Congress of the Hungarian Biological Society*, 27–29 June 1984, Veszprém, Abstracts.
Rimóczi, I. 1985a: Soil analysis of locality of *Langermannia gigantea* (Batsch ex Pers.) Rostk. — *IXth International Symposium on soil biology*, Sopron, 1985. 27–30. August, Abstracts
Rimóczi, I. 1985b: Talajvizsgálatok az óriás pöfeteg (Langermannia gigantea (Batsch ex Pers.) Rostk. termőhelyén és környezetében. (Soil studies on the biotops of the Langermannia gigantea [Batsch ex Pers.] Rosk. and surroundings.) — *Mikol. Közlem.*, **3:** 137–150.
Rimóczi, I. 1987: Az óriás pöfeteg (Langermannia gigantea (Batsch ex Pers.) Rostk.) növekedésének és fejlődésének összefüggése a klímatikus tényezőkkel. (Growth and development of the giant puff-ball and their correlation to the climatic factors.) — *Mikol. Közlem.* **5.**
Runck, G. 1973: Eine Mitteilung aus der Pfalz. — *Südwestdeutsche Pilzrundschau*, **9:**/2: 10.
Runge, A. 1971: Zur Verbreitung des Riesenbovistes in Westfalen. — *Natur und Heimat*, **31.**/1: 44–47.
Runge, A. 1976: Weitere Funde des Riesenbovistes in Westfalen. — *Natur und Heimat*, **36**/2: 29–32.
Smarda, F. 1972: Pilzgesellschaften einiger Laubwälder Mährens. — *Acta Sci. Nat. Acad. Sci. Bohemoslovacae*, Brno, **6:** 1–53.
Soó, R. 1964, 1966, 1968, 1970, 1973, 1980: A magyar flóra és vegetació rendszertani-, növényföldrajzi kézikönyve. I–VI. (Synopsis systematico-geobotanicum florae vegetationisque Hungariae. I–VI.) Budapest.
Sous-Dorn, B. 1979: Erste Versuche zur Domestikation des Riesenbovisten, *Calvatia gigantea* (Batsch ex Persoon) Lloyd. — *Mitteilungen der Versuchsanstalt für Pilzanbau der Landwirtschaftskammer Rheinland Krefeld-Großhüttendorf*, **3:** 31–35.
Sukopp, H. 1969: Der Einfluß des Menschen auf die Vegetation. — *Acta Geobotanica*, **17:** 360–371.
Szemere, L. 1968: A Bakony-hegység nagygombái (Höhere Pilze des Bakony-Gebirges). — *A Veszprém Megyei Múzeumok Közleményei*, **7:** 147–170.
Ubrizsy, G. 1957: Újabb vizsgálatok az erdőtípusok talajlakó nagygombáinak társulási viszonyairól (Further studies on the sociology of the terestrial mushrooms in different forest types.) — *Ann. Inst. Prot. Plant. Hung.*, **7:** 409–441.

Takács, B., Siller, I. 1980: A Bükk hegységi Ősbükkös nagygombái. (Macromycetes of the Ősbükkös Conservation Area in the Bükk Mountains.) — *Mikol. Közlem.*, **3:** 121–132.
Teng. S. C. 1964: *Fungi from China.* Peking.
Terpó, A., E. Bálint, K. 1983: Növényfajok elterjedése, az emberi hatások befolyása a termőhelyekre. (Plant areas and human influence on the biotops.) — *Kertészeti Egyetem*, Budapest.
Terpó, A., Rimóczi, I., Tasnádi, G. 1984: Carolus Clusius, the founder of mycology in Europe and initiator of the Hungarian mushroom research. — *Internat. Symp. on Substrates for Mushroom Growing and Cultivation of Pleurotus Species*, 23–25. Okt. 1984. Budapest, Summaries.

Acta Botanica Hungarica 33 (3—4), pp. 295—300 (1987)

MACENTINA BORHIDII, EINE NEUE FOLIICOLE FLECHTE AUS TANSANIA*

EDIT FARKAS[1] und ANTONÍN VĚZDA[2]

[1] INSTITUT DER ÖKOLOGIE UND BOTANIK DER UNGARISCHEN AKADEMIE DER WISSENSCHAFTEN, VÁCRÁTÓT
[2] BOTANISCHES INSTITUT DER TSCHECHOSLOWAKISCHEN AKADEMIE DER WISSENSCHAFTEN, PRŮHONICE BEI PRAHA

(Eingegangen: 12 Juni, 1987)

Eine neue foliicole Art der Gattung *Macentina* Vězda (Verrucariaceae), *M. borhidii* sp. n., wird beschrieben und abgebildet; kennzeichnend für die mit Typus-Art der Gattung, *M. perminuta* Vězda, verwandte Art ist der isidiöse Thallus. Die bisher 5 bekannten *Macentina*-Arten werden in Schlüsselform zusammengestellt.

In einer Kollektion foliicoler Flechten aus Tansania (Tanga Region, Usambara-Gebirge) gesammelt von den jüngeren Autor (E. F.) im Herbst 1986, wurden mehrmals sehr dünne mit isidiösen Vermehrungsorganen versehene Thalli gefunden. Erst nach der Untersuchung der ganzen Aufsammlung von tausenden Blättern ist es den Autoren gelungen, auch Thalli mit Fruchtkörpern zu entdecken. Die winzig kleinen perithecioiden Ascomata stimmen im Aufbau weitgehend mit *Macentina perminuta* Vězda überein, der Typusart der Gattung *Macentina* Vězda. Nach sorgfältiger mikroskopischer Untersuchung des reichen Belegmaterials bestand kein Zweifel, daß es sich um eine neue Art der Gattung *Macentina* handelt. Sie wird in folgenden als *Macentina borhidii* sp. n. beschrieben.

Die den Verrucariaceen zugeordnete Gattung *Macentina* wurde von VĚZDA 1973: 69 vorgestellt, begründet auf die foliicole Art, *M. perminuta* Vězda aus Guinea (West-Afrika). Kennzeichnend für die Gattung ist die Merkmalskombination von perithecioiden Ascomata mit einfach gebauten hellen Wänden ohne Involucrellum, Fehlen von Paraphysoiden, aber Vorhandensein von Periphysoiden, fissitunicaten, 8-sporigen Asci, hyalinen, querseptierten Ascosporen und Algen vom *Trentepohlia*-Typ.

Neben dem Typus wurden später weitere drei Arten beschrieben: *M. abscondita* Coppins et Vězda 1977: 47, auf Rinde von *Sambucus* in Großbritannien gefunden, *M. hepaticola* Döbbeler et Vězda 1982: 2, eine lebermoosbewohnende Art aus Zaire, und *M. aurantiaca* McCarthy et Vězda 1985: 289, auf *Sambucus*-Borke von West-Irland.

Um einen Vergleich der neuen *Macentina borhidii* mit dem Typus und den anderen Arten zu ermöglichen, seien alle Arten kurz in Schlüsselform zusammengestellt.

* Usambara Rain Forest Research Project Publications No. 7.

1a Ascomata hellbraun, braun oder gelblich, bis 0.2 mm breit, Ascosporen 3-septiert.
  2a Foliicole Arten, Afrika. Ascomata 0.1—0.2 mm breit.
    3a Thallus ohne Isidien. Ascomata 0.1—0.15 mm breit, Ascosporen 16—23/3.5—4 μm. Guinea und Zaire.
    M. perminuta Vězda

    3b Thallus mit kugeligen bis obkonischen, 50—70 μm breiten, hellgrünen Isidien. Ascomata 0.15—0.2 mm breit, Ascosporen 18—23/4.5—5 μm. Tansania.
    M. borhidii (sp. n.)
  2b Nicht foliicole Arten.
    4a Auf dem epiphyllen Lebermoos *Radula flaccida*. Ascomata 0.14—0.2 mm breit, im oberen Teil mit einem ringförmigen Kragen versehen, gebildet aus dickwandigen, borstenartigen Hyphen.
    Ascosporen 3-septiert, 18—24/4—5 μm. Zaire.
    M. hepaticola Döbb. et Vězda

    4b Rindenbewohnend. Ascomata 0.08—0.12 mm breit, Ascosporen 12—20/3.5—4.5 μm. Großbritannien.
    M. abscondita Coppins et Vězda

1b Ascomata orangerot, 0.2—0.35 mm breit. Ascosporen (6—) 7 (—15)- septiert, nm 46/5.6 μm. Rindenbewohnend in W-Irland.
M. aurantiaca McCarthy et Vězda

Macentina borhidii* Farkas et Vězda sp. n.

Thallus epiphyllus, tenuissimus, cinereoviridis, hyphis hyalinis supra cuticulam foliorum repentibus, algas involventibus, formatus, isidiis subglobosis vel obconicis, 50–70 μm crassis, pallide viridibus instructus. Isidia ecorticata, cellulis algarum gregatis hyphisque parce immixtis formata. Algae chlorococcales cellulis globosis vel mutua pressione difformibus, 5–7 μm crassis.

Ascomata hemisphaerica vel doliiformia, basi constricta ad thallum adnata, pallide fuscolutea, in aetate fusca, hyphis primum laxis incoloratis tecta, demum ± glabra. Paries ascomatum 10–15 μm crassus, incoloratus, hyphis tangentialiter extensis, basin versus subparenchymatice contextus. Periphysoides copiosae, circa 15 μm longae, septatae, membranis gelatinosis. Paraphysoides nullae. Asci fissitunicati, cylindrico-ellipsoidei, membranis in apice incrassatis, in maturitate leptodermaticis, 8-spori. Ascosporae ellipsoideae, hyalinae, rectae vel leviter curvulae, 3-septatae, 18–23/4.5–5 μm.

Icon.: Fig. 1 (anatomia).

Hab.: Tansania, "Tanga Region, East-Usambara Mts., Kihuhwi Forest Reserve, in lowland to intermediate rainforest along a forest path leading from Kihuhwi to Kwamkoro, at 220–320 m alt., 3 Nov. 1986, coll. Farkas E. no. 86228/LD" (Holotyp: VBI; Isotypen: Herb. Dept. of Forest Biol. Sokoine Univ. Agr., Morogoro; GZU; UPS; Exsicc. Vězda, Lich. Sel. 2276); ibid.: "Mtai Forest Reserve, dry semideciduous forest and secondary dry vegetation on the E slopes of Mtai ridge, W of Maramba village, at 250–500 m alt., 13 Nov. 1986, coll. Farkas E. no. 86245/LC; ibid.: Amani East Forest Reserve, above Sigi river bridge, streamside vegetation and wet lowland type rainforest, at 470–500 m alt., 8 Nov. 1986, coll. Borhidi A.

* Zur Ehren des verdienten ungarischen Botanikers, Dr. A. Borhidi genannt.

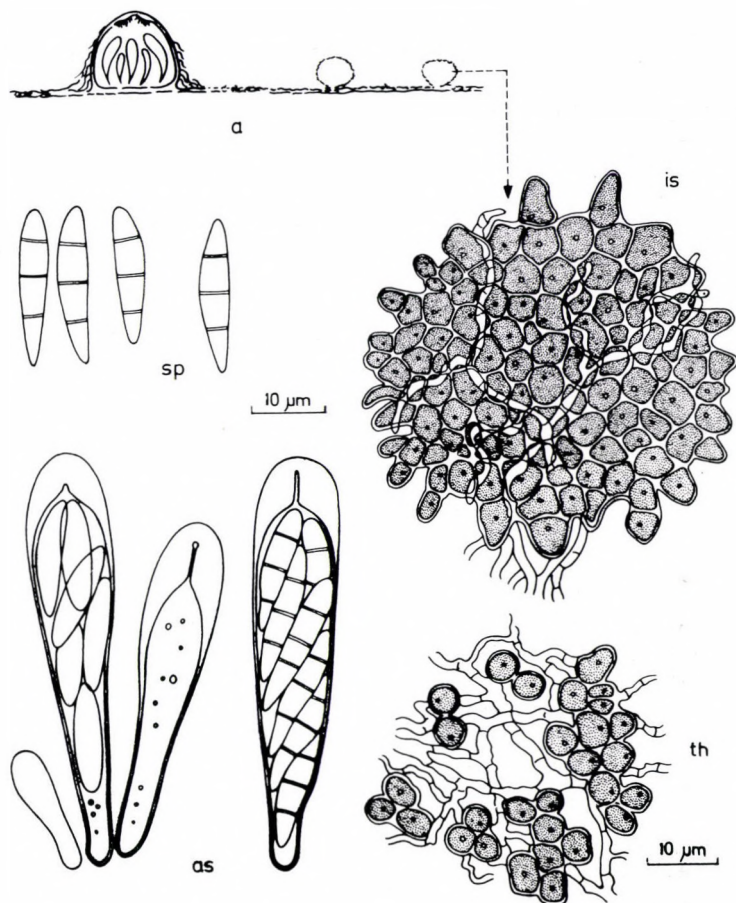



Abb. 1. — *Macentina borhidii* Farkas et Vězda sp.n. (Orig. Koll.). *a* Vertikalschnitt durch ein Ascomatum und zwei Isidien, *as* Asci, links unreif, recht reif, *is* Ein Isidium (Vertikalschnitt), *sp* Ascosporen, *th* Thallus (im Aufsicht)

Farkas E. and Pócs T. no. 86236/LA; ibid.: in wet rainforest along Derema road, 1.5 km NE of Amani, below Chemka and Sigi river tributary, at 770 m alt., 8 Nov. 1986, coll. Farkas E. no. 86234/LE; ibid.: Amani — Sigi Forest Reserve, intermediate rainforest along Sigi and Ngurue rivers and the N slopes above them, 420–600 m alt., 30 Oct. 1986, coll. Borhidi A. and Farkas E. 86219/LD. — West-Usambara Mts., Shagayu Forest Reserve, tributary of Umba river below Kwashemhambu, 6 km NW of Mlalo village in wet type of intermediate rain forest at 1600–1700 m alt., 21 Oct. 1986, coll. Farkas E. no. 86203/LA; ibid.: SW of Ambangulu Tea Estate, on the ridge above the S escarpment in the submontane rain forest, at 1200–1400 m alt., 23 March 1984, coll. Borhidi A. and Pócs T. no. 8455/BL (Alle Belege VBI).

Beschreibung. Lager epiphyll, sehr dünn und manchmal unauffällig, hell graugrün, gebildet aus einen, den Blattoberflächen dicht anliegenden, weitmaschigen Netz von farblosen Hyphen mit grünen, kugeligen oder durch gegenseitigen Druck verformten, 4–7 μm breiten Algenzellen vom *Trebouxia*-Typ; sie liegen auf oder in dem Hyphennetz einzeln, meist aber in relativ wenigzelligen Gruppen, ohne eine geschlossene Algenschicht zu bilden. Ausgenommen eine enge Randzone trägt das Lager zahlreiche, kugelige oder obkonische, 50–70 μm breite, hellgrüne Isidien.

Auf ersten Blick erinnern die Isidien der neuen Art an die der foliicolen Flechten *Bacidia scutellifera* Vězda 1975: 421 oder *Phyllophiale alba* R. Sant. 1952: 558. Es handelt sich aber nur um analoge Organe, die sich von den anatomisch kompliziert gebauten, meist durch den Mykobionten geformten Isidien der letztgenannten Arten weitgehend unterscheiden. Im anatomischen Bau erweist sich ein Isidium von *M. borhidii* als eine Kolonie von zahlreichen Algenzellen, die von relativ wenigen, an die Algenzellen angepreßten Hyphen durchzogen werden. Die Hyphen bilden keine Hyphenrinde oder Hüll um die Kolonien. Die Oberfläche der Isidien sieht im Mikroskop etwas höckerig aus, verursacht durch die nach außen gewölbten Algenzellen. Die Isidien sind mit wenigen Hyphen auf der Lageroberfläche befestigt; sie werden von außen passiv vom Lager losgebrochen: ohne Zweifel dienen sie zur vegetativen Fortpflanzung und Verbreitung der Flechte.

Trotz des einfachen inneren Baus lassen sich die Isidien von *M. borhidii* nicht als »primitive« Organe bezeichnet. Die einheitliche Form und Größe und die regelmäßige Anordnung auf dem Lager sprechen für eine hohe Spezialisation im Hinblick auf die vegetative Fortpflanzung, die in diesem Konstruktion bei anderen foliicolen und wahrscheinlich auch anderen Flechten bisher nicht beobachtet wurde.

Ascomata wurden nur einigemal im Material gefunden. Sie stehen in den zentralen Partien des Lagers, meist in geringer Zahl (höchstens 10 Fruchtkörper auf einem Lager). Sie sind halbkugelig bis tonnenförmig, an der Basis verschmälert dem Lager aufsitzend, 0,15–0,20 mm breit und ebenso hoch oder etwas höher, hell gelbbraun, alte Ascomata braun, mit unauffälligem, punktförmigem Ostiolum. Rings um das Ostiolum ist die Oberfläche kahl, sonst ist sie mit vertikal orientierten farblosen Hyphen bedeckt; die Hyphen bilden ein weitmaschiges Netz, Rest eines dichten algenfreien Hyphenknäuels, in dem sich die Ascomata-Anlage bildet; bei älteren Ascomata treten sie zurück. — Gehäuse im Schnitt mit 10–15 μm dicker Wand aus tangential gestreckten Zellen gebildet; nach außen sind die Zellen abgerundet. Periphysoiden zahlreich ausgebildet, bis 15 μm lang, mit stark gelatinös aufquellenden Wänden, vom Gehäuse radiär ins Innere strahlend. Paraphysoiden fehlen auch in unreifen Ascomata. Asci verlängert-ellipsoidisch bis zylindrisch, in einem kurzen Fuß verschmälert, fissitunicat, mit auffälligen Apikalverdickungen, bei der Reife Exotunica zart; 8-sporig, Ascosporen ellipsoidisch bis fast spindelig, gerade oder leicht gebogen, farblos, 3-septiert, 18–23/4,5–5 μm. Jod (Lugolsche Lösung) färbt die Hymenialgallerte lachsrot.

In allen Aufsammlungen wächst die Flechte epiphyll auf relativ großen Laubblättern ohne Begleiter oder mit nur wenigen vergesellschafteten Flechten zusammen. Auf Blättern mit gut entwickelten Lagern anderer Flechten fehlt sie völlig. Offensichtlich gehört M. borhidii zu den foliicolen Pionierarten, die dank ihrer zahlreichen Isidien sich schnell auf den neuen Blättern ansiedeln kann; ihr Lebenszyklus ist daher auch im Vergleich mit anderen relativ kurzlebigen foliicolen Flechten sehr kurz.

Discussion

Von den nun 5 beschriebenen *Macentina*-Arten sind 2 obligat foliicol: *M. perminuta* (Typus der Gattung) und *M. borhidii*. Beide sind sehr nahe verwandt; im Bau ihrer Fruchtkörper lassen sich nur kleine, kvantitative Unterschiede feststellen. Die Ascomata von *M. perminuta* sind etwas kleiner (0,1–0,15 mm) als die bei *M. borhidii* (0,15–0,20 mm). Das weitmaschiges Netz von hyalinen Hyphen um die Ascomata von *M. borhidii* fehlt bei dem Typus sowie bei den reich belegten Proben aus Zaire von *M. perminuta*, was

sich durch das Fehlen von jungen Ascomata erklären läßt. Auch bei älteren Fruchtkörpern von *M. borhidii* können sie fehlen. Im Innenbau der Fruchtkörper stimmen beide Arten fast völlig überein; die etwas kleineren Dimensionen der Ascosporen bei *M. perminuta* (siehe Bestimmungsschlüssel) spielen dabei als Unterscheidungsmerkmal eine geringere Rolle. Was aber beide Arten grundsätzlich unterscheidet, sind die Isidien. Trotz neuer eingehender Untersuchung an den Typenmaterial und den zwei zahlreichen Belegen von *M. perminuta* wurden auf ihren Lagern keine Isidien oder ähnliche Organe gefunden. Demgegenüber fehlen sie nie aus den Lagern von *M. borhidii.* Hier ist zu betonen, daß die so reich in den Kollektionen aus O-Usambara vorhandenen isidiösen Thalli von *M. borhidii* gewöhnlich steril sind; nur dank des reichen Aufsammlungen von tausenden Blättern ist es gelungen, auch fruchtende Thalli zu finden un damit die isidiösen sterilen Thalli zu identifizieren.

Aus oben vorgelegten Vergleich ergibt sich weiters, daß diese zwei Arten — als erster Nachweis von pyrenocarpen Flechten — dem Konzept der Artenpaare von Poelt (1970: 187–198) entsprechen. Die fruchtende, stets isidienlose *M. perminuta* als Primärart, die isidiöse, nur selten fruchtende *M. borhidii* als Sekundärart. Nach den bisherigen Kenntnisstand sind Partner dieser Paare geographisch getrennt. *M. perminuta* wurde bisher in Guinea (W-Afrika) und Zaire (Central-Afrika) gefunden; sie gehört zu den seltenen Arten angesichts der Tatsache, daß sie nur 3× in Kollektionen von tausenden Blättern gefunden wurde. *M. borhidii* ist bisher nur aus Usambara (Tansania Ost-Afrika) bekannt. Die sterilen, isidiösen Thalli wurden vielmals gefunden; im Vergleich mit der Zahl der anderen Flechtensippen in den tansanischen Kollektionen, erweist sich die Art als häufig für das Gebiet.

Du Rietz (1924) bezeichnete als Isidien »alle kleineren Thallusauswüchse, die Gonidien erhalten«. Wir haben mit gewissen Zögern die eigenartigen, kugeligen oder obkonischen Vermehrungsorgane von *M. borhidii* mit dem Terminus Isidien bezeichnet. Wir stoßen dabei auf ähnliche Probleme, wie sie von Santesson (1952: 558) für die Vermehrungsorgane von Phyllophiale alba diskutiert worden sind: darf man diese Organe als Lagerauswüchse bezeichnen oder handelt es sich um höher organisierte, spezielle Vermehrungsorgane ? Ein vergleichbarer Beispiel zu diesem Problem sind die Isidien der foliicolen *Bacidia scutellifera:* die schildförmigen, kurzgestielten Organe sind mit einem speziellen Abwurfapparat versehen (Vězda 1975: 421). Die Lösung dieser Frage liegt aber nicht mehr in Rahmen dieser Arbeit.

LITERATUR

Coppins B. J. et Vězda A. 1977: *Macentina*, a lichen genus new to Europe. *Lichenologist* **9:** 47–49.

Döbbeler P. et Vězda A. 1982: *Macentina hepaticola*, eine neue Flechte aus Zaire. *Mitt. Bot. München* **18:** 1–8.

Du Rietz G. E. 1924: Die Soredien und Isidien der Flechten. *Svensk Bot. Tidskr.* **18.**

McCarthy P. M. et Vězda A. 1985: *Macentina aurantiaca*, a new lichen from the Burren, Western Ireland. *Lichenologist* **17:** 289–291.

Poelt J. 1970: Das Konzept der Artenpaare bei den Flechten. *Dtsch. Bot. Ges. Neue Folge*, **4:** 187–198.

Vězda A. 1973: Foliicole Flechten aus der Republik Guinea (W-Afrika). *Acta Mus. Silesiae, Opava, ser. A*, **22:** 67–90.

Vězda A. 1975: Foliicole Flechten aus Tanzania. *Folia Geobot. Phytotax., Praha*, **18:** 383–432.

Acta Botanica Hungarica 33 (3–4), pp. 301–303 (1987)

STUDIES IN *RONDELETIEAE* (RUBIACEAE) X.

NEW COMBINATIONS OF CENTRAL AMERICAN TAXA

A. BORHIDI

INSTITUTE OF ECOLOGY AND BOTANY, HUNGARIAN ACADEMY OF SCIENCES H-2163, VÁCRÁTÓT, HUNGARY

(Received: 15 March 1987)

A taxonomic review of the Central American *Rondeletia* species was carried out according the criteria proposed in the "Studies in Rondeletieae (Rubiaceae) III" of the same author published in the Acta Botanica Hungarica 28: 65–71 (1982). Twenty-eight taxa of the genus *Rondeletia* are to be transferred into the genera *Rogiera* Planch. and *Arachnothryx* Planch., respectively. The proposed new combinations are the following:

Rogiera aprica (Lundell) Borhidi comb. nova — Mexico,
Basionym.: *Rondeletia aprica* Lundell Contrib. Univ. Mich. Herb. **7:** 52. 1942.

Rogiera backhousii (Hook. f.) Borhidi comb. nova — Honduras,
Basionym.: *Rondeletia backhousii* Hook. f. Bot. Mag. **III. 33.** tab. 6290. 1877.

Rogiera brachystantha (Standl. et Steyerm.) Borhidi comb. nova — Guatemala,
Basionym.: *Rondeletia brachystantha* Standl. et Steyerm. Publ. Field Mus. Nat. Hist. Chicago Ser. Bot. **23:** 25. 1943.

Rogiera chiapasensis (Standl.) Borhidi comb. nova — Mexico,
Basionym.: *Rondeletia chiapasensis* Standley Publ. Field Mus. Nat. Hist. Chicago Bot. Ser. **22:** 54 1940.

Arachnothryx brenesii (Standl.) Borhidi comb. nova — Costa Rica,
Basionym.: *Rondeletia brenesii* Standley Publ. Field Mus. Nat. Hist. Chicago Bot. Ser. **18:** 1370. 1938.

Arachnothryx buddleioides (Benth.) Planch. var. aspera (Kirkbr.) Borhidi comb. nova — Central America,
Basionym.: *Rondeletia buddleioides* var. *aspera* Kirkbride Ann. Mo. Bot. Gard. **55:** 378. 1968.

Arachnothryx chinajensis (Standl. et Steyerm.) Borhidi comb. nova — Guatemala,
Basionym.: *Rondeletia chinajensis* Standl. et Steyerm. Publ. Field Mus. Nat. Hist. Chicago Bot. Ser. **23:** 254. 1947.

Arachnothryx cordovana (Standl. et Steyerm.) Borhidi comb. nova — Guatemala,
Basionym.: *Rondeletia cordovana* Standl. et Steyerm. Publ. Field Mus. Nat. Hist. Chicago Bot. Ser. **23:** 26. 1943.

Arachnothryx edwardsii (Standl.) Borhidi comb. nova — Honduras,
Basionym.: *Rondeletia edwardsii* Standl. Trop. Woods No. **37:** 31 1934.

Arachnothryx gonzalaeoides (Standl.) Borhidi comb. nova — Mexico,
Basionym.: *Rondeletia gonzalaeoides* Standley Publ. Field Mus. Nat. Hist. Chicago, Bot. Ser. **8:** 160. 1930.

Arachnothryx gracilispica (Standl.) Borhidi comb. nova — Mexico,
Basionym.: *Rondeletia gracilispica* Standley Publ. Field Mus. Nat. Hist. Chicago, Bot. Ser. **8:** 342. 1931.

Arachnothryx izabalensis (Standl. et Steyerm.) Borhidi comb. nova — Guatemala,
Basionym.: *Rondeletia izabalensis* Standl. et Steyerm. Publ. Field Mus. Nat. Hist. Chicago, Bot. Ser. **22:** 286. 1940.

Arachnothryx liebmanii (Standl.) Borhidi comb. nova — Mexico,
Basionym.: *Rondeletia liebmanii* Standley Journ. Wash. Acad. Sci. **17:** 336. 1927.

Arachnothryx lundelliana (Standl.) Borhidi comb. nova — Brit. Honduras,
Basionym.: *Rondeletia lundelliana* Standl. Contrib. Univ. Mich. Herb. No. **4:** 31. 1940.

Arachnothryx macrocalyx (Standl. et Steryerm.) Borhidi comb. nova — Guatemala,
Basionym.: *Rondeletia macrocalyx* Standl. et Steyerm. Publ. Field Mus. Nat. Hist. Chicago, Bot. Ser. **23:** 254. 1947.

Arachnothryx mexiae (Standl.) Borhidi comb. nova — Mexico,
Basionym.: *Rondeletia mexiae* Standl. Publ. Field Mus. Nat. Hist. Chicago, Bot. Ser. **22:** 55. 1940.

Arachnothryx myriantha (Standl. et Steyerm.) Borhidi comb. nova — Guatemala, Mexico,
Basionym.: *Rondeletia myriantha* Standl. et Steyerm. Publ. Field Mus. Nat. Hist. Chicago, Bot. Ser. **22:** 288. 1940.

Arachnothryx nebulosa (Standl.) Borhidi comb. nova — Honduras,
Basionym.: *Rondeletia nebulosa* Standley Trop. Woods No. **37:** 32. 1934.

Arachnothryx oaxacana (Standl.) Borhidi comb. nova — Mexico,
Basionym.: *Rondeletia oaxacana* Standl. Publ. Field Mus. Nat. Hist. Chicago, Bot. Ser. **11:** 255. 1936.

Arachnothryx phyllocephala (Standl. et L. O. Wms.) Borhidi comb. nova — Honduras,
Basionym.: *Rondeletia phyllocephala* Standl. et L. O. Wms. Ceiba, **3:** 63. 1952.

Arachnothryx skutchii (Standl. et Steyerm.) Borhidi comb. nova — Guatemala,
Basionym.: *Rondeletia skutchii* Standl. et Steyerm. Publ. Field Mus. Nat. Hist. Chicago, Bot. Ser. **22:** 289. 1940.

Arachnothryx standleyana (A. Molina) Borhidi comb. nova — Honduras,
Basionym.: *Rondeletia standleyana* A. Molina Ceiba, **1:** 262. 1951.

Arachnothryx stenostachya (Standl.) Borhidi comb. nova — Costa Rica,
Basionym.: *Rondeletia stenostachya* Standley Publ. Field Mus. Nat. Hist. Chicago. Bot. Ser. **18:** 1372. 1938.

Arachnothryx tacanensis (Lundell) Borhidi comb. nova — Guatemala,
Basionym.: *Rondeletia tacanensis* Lundell Bull. Torr. Bot. Cl. **66:** 603. 1939.

Arachnothryx torresii (Standl.) Borhidi comb. nova — Costa Rica,
Basionym.: *Rondeletia torresii* Standl. Journ. Wash. Acad. Sci. **18:** 163. 1928.

Arachnothryx vulcanicola (Standley et Steyerm.) Borhidi comb. nova — Guatemala,
Basionym.: *Rondeletia vulcanicola* Standl. et Steyerm. Publ. Field Mus. Nat. Hist. Chicago, Bot. Ser. **22:** 291. 1940.

Arachnothryx zolleriana (Standl. et Steyerm.) Borhidi comb. nova — Guatemala,
Basionym.: *Rondeletia zolleriana* Standl. et Steyerm. Publ. Field Mus. Nat. Hist. Chicago, Bot. Ser. **22:** 292. 1940.

REFERENCES

Borhidi, A. 1982: Studies in Rondeletieae (Rubiaceae) III. The genera *Rogiera* and *Arachnothryx*. *Acta Bot. Hung. Acad. Sci. Hung.* **28:** 65–71.

Standley, P. C. 1930: Studies on American plants IV. *Publ. Field. Mus. Nat. Hist. Chicago, Bot. Ser.* **8:** 133–236.

Standley, P. C. 1931: Studies on American plants V. *Ibidem* **8:** 295–398.

Standley, P. C. 1936: Studies on American plants VI. *Ibidem* **11:** 145–276.

Standley, P. C. 1938: *Rondeletia* L. in: Flora of Costa Rica. *Ibidem* **18:** 1369–1373.

Standley, P. C. 1940: Studies on American plants IX. *Ibidem* **22:** 1–62.

Standley, P. C., Steyermark, J. A. 1943: Studies on Cntral American plants I. *Ibidem* **22:** 219–322.

Standley, P. C., Steyermark, J. A. 1947: Studies on Central American plants, III. *Ibidem* **23:** 3–28.

Acta Botanica Hungarica 33 (3—4), pp. 305—316 (1987)

CHROMOSOME MORPHOLOGY AND DNA CONTENT IN THE SYSTEMATICS OF THE *SCILLA BIFOLIA* AGGREGATE

Z. KERESZTY

INSTITUTE OF ECOLOGY AND BOTANY, HUNGARIAN ACADEMY OF SCIENCES, H-2163 VÁCRÁTÓT, HUNGARY

(Received: 1 May 1987)

Twenty-two *Scilla bifolia* s.l. populations from Hungary were investigated cytotaxonomically for their taxonomical revision, including the karyotype analysis and the determination of C-Banding pattern and DNA content. For evaluating the idiograms of the karyotypes, a statistical analysis was used to reveal tendencies of karyometric differences among the taxa. According to the results in Hungary there are 4 species in the *Scilla bifolia* aggregate on 3 ploidy level: *S. vindobonensis; S. kladnii* (diploids), *S. drunensis* (tetraploid) and *S. spetana* (hexaploid). Within *S. vindobonensis* one variety and one subspecies were separated. Up till now *S. buekkensis* have been known as a separate species. Our results show that it does not differ significantly from *S. drunensis*. Therefore *S. buekkensis* should be considered as a subspecies of *S. drunensis*. The cytotaxonomical results are confirmed by morphological and biostatistical studies.

Introduction

At the Biosystematic Conference on the Northern European Flora (BORHIDI 1985, KERESZTY *et al.* 1986) and in KERESZTY 1987 presented cytological studies on the South East European populations of the *Scilla bifolia* aggregate. It was suggested that the taxonomic revision of this phenotypically rather uniform but genotypically highly varied group requires more thorough cytological and cytotaxonomical methods.

GREILHUBER and SPETA (1977) indicated that the karyotype, the C-Banding pattern and the DNA content show differences of taxonomic importance in this species group. In order to confirm this statement, twenty-two populations from fifteen major regional units of Hungary were subjected to a more detailed cytotaxonomic analysis, in agreement with other morphological and phenological studies of the same taxa. The results of new karyotype analyses and the determination of C-Banding pattern and DNA content are presented here.

Material and methods

The material consisted of root-tip samples taken between October and January from populations planted in the experimental site of the Institute. Cytological investigations were made as before (KERESZTY and SZILÁGYI 1984). For evaluating the idiograms of the karyotypes, an appropriate computer program was used to outline the idiograms and their centromer-index (CI) curves. The C-Banding analyses were performed in co-operation with the Botanical Research Institute of the University of Vienna, in Dr. GREILHUBER's laboratory. 20 root-tip preparations per population were analysed with special Giemsa C-Banding technique (GREILHUBER and SPETA 1977). The method for the determination of DNA content represented in GREILHUBER and KERESZTY 1988.

Results and discussion

The ploidy levels detected earlier are now confirmed: 2n = 18, 2n = 36 2n = 54. The karyotypes of diploid populations occurring at the lowland along the river Danube are very similar with their conspicuous one pair of SAT-chromosomes and three pairs of metacentric chromosomes. They agree with

Table 1

Significance test of $\overline{M}$ and $\overline{AR}$ data of Hungarian Scilla taxa at 1% significance level (Ø = nonsignificant)

a. $\overline{M}$ and $\overline{AR}$ data and their variances

	sampl.	$\overline{M}$ u	var.	sampl.	$\overline{AR}$	var.
S. vindobonensis v. vindobonensis	6	12.6	0.53	7	2.48	0.0212
S. vind. v. transdanubialis	6	15.0	0.84	6	2.45	0.0109
S. vind. ssp. borhidiana	6	9.1	0.26	6	2.43	0.0032
S. kladnii	6	9.6	0.08	6	3.84	0.0345
S. drunensis	5	7.1	0.10	5	1.99	0.0305
S. drunensis ssp. buekkensis	5	11.3	0.33	5	1.92	0.0104
S. spetana	5	8.8	0.13	5	1.37	0.0050

b. Significant differences of $\overline{M}$ data

	spetana	*buekkensis*	*drunensis*	*kladnii*	*borhidiana*	*trans-danubialis*
vindobonensis	3.9+−1.17	1.3+−1.31	5.5+−1.15	3.0+−1.01	3.5+−1.15	2.4+−1.52
trans-danubialis	6.1+−1.33	3.7+−1.54	7.9+−1.30	5.4+−1.24	5.8+−1.35	
borhidiana	Ø	2.2+−1.06	2.0+−0.85	Ø		
kladnii	0.8+−0.64	1.7+−0.86	2.5+−0.59			
drunensis	1.7+−0.73	4.2+−0.98				
buekkensis	2.5+−1.01					

c. Significant differences of $\overline{AR}$ data

	spetana	*buekkensis*	*drunensis*	*kladnii*	*borhidiana*	*trans-danubialis*
vindobonensis	1.11+−0.23	0.54+−0.24	0.49+−0.29	1.36+−0.29	Ø	Ø
trans-danubialus	1.08+−0.18	0.53+−0.20	0.46+−0.28	1.40+−0.28	Ø	
borhidiana	1.07+−0.13	0.52+−0.15	0.44+−0.26	1.41+−0.25		
kladnii	2.48+−0.27	1.93+−0.30	1.85+−0.36			
drunensis	0.62+−0.28	Ø				
buekkensis	0.55+−0.18					

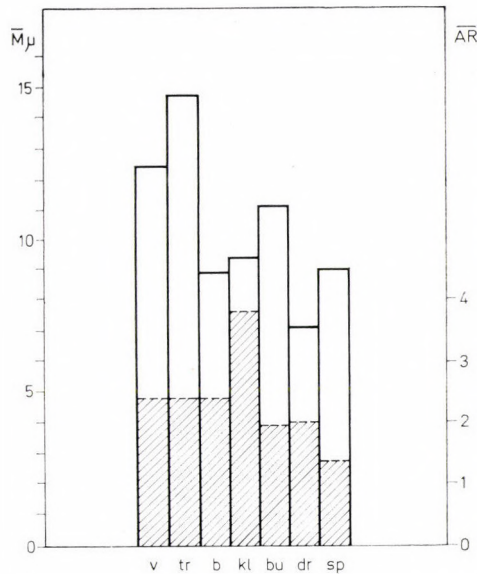



Fig. 1. Average length ($\overline{M}$) and arm-ratio ($\overline{AR}$) values of the chromosomes of the studied *Scilla*-taxa. — $\overline{M}$ = white column, $\overline{AR}$ = dashed column, v = *Scilla vindobonensis* var. *vindobonensis*, tr = *S. vindobonensis* var. *transdanubialis*, b = *S. vindobonensis* ssp. *borhidiana;* kl = *S. kladnii;* bu = *S. drunensis* ssp. *buekkensis;* dr = *S. drunensis* ssp. *drunensis;* sp = *S. spetana*

the karyotype of *Scilla vindobonensis* and differ from that of *Scilla bifolia* (cf. KERESZTY and SZILÁGYI 1984). *Scilla kladnii* growing in the north-eastern part of Hungary and the East Carpathians differs from *Scilla bifolia* by its one pair of meta- and one pair of telocentric chromosomes. In the karyotype of polyploids well stained satellites are very rarely found, and the number of metacentric pairs is 2 or 5 (cf. KERESZTY and SZILÁGYI 1986). With an increase in the ploidy level, a gradual shortening of the chromosomes can be observed. A comparative study of the average length ($\overline{M}$) and arm-ratio ($\overline{AR}$) of the chromosomes indicated significant differences as demonstrated in Table 1 (cf. KERESZTY 1987). In the Fig. 1 the $\overline{M}$ data are indicated on the left, the $\overline{AR}$ data on the right scale. The length of columns corresponds to the average length of chromosomes and the dashed parts represent the arm-ratio. It is clearly seen that for species the $\overline{AR}$ is significant; whereas $\overline{M}$ is characteristic of the infraspecific taxa. The results suggest that tetraploids should not be separated at the species level.

Figures 2–3 show the CI curves of chromosomes of 4 diploid taxa ranged according to the arm-ratio and to chromosome pairs. Three of them, having similar curves, belong to *S. vindobonensis*. Smaller or greater differences in details represent lower or higher infraspecific ranks. The CI curve of the *S.*

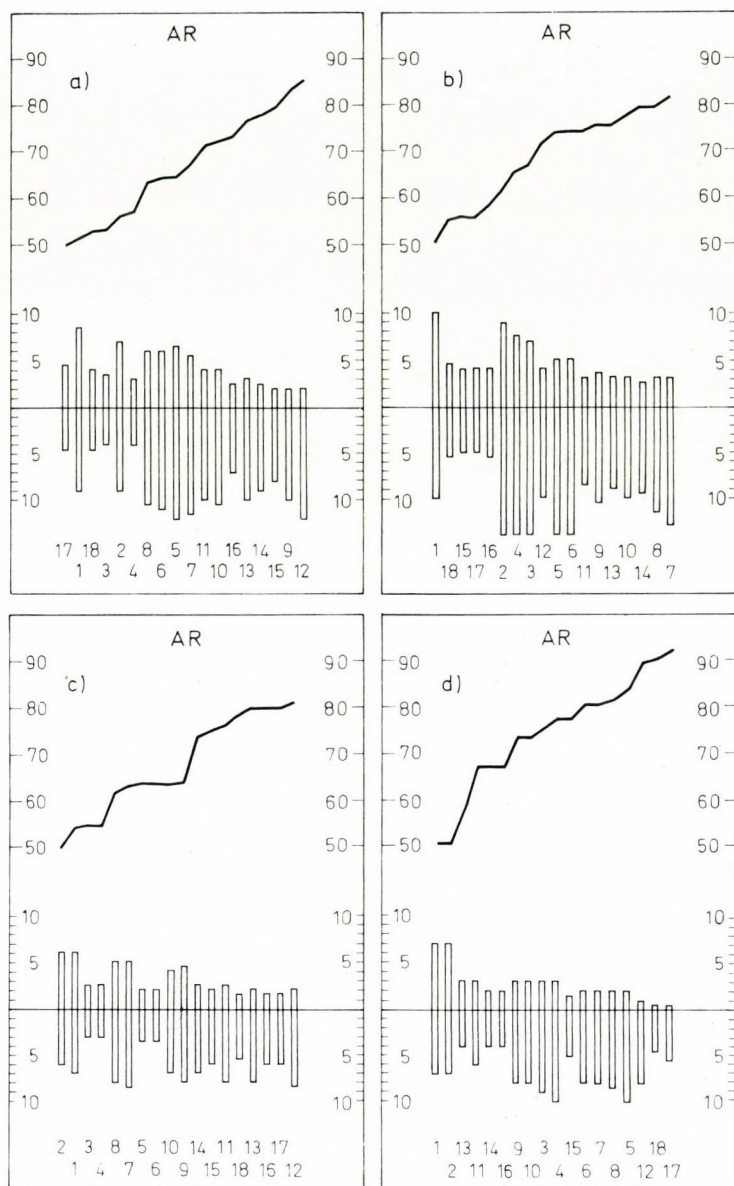



Fig. 2. Centromer-index curves of the Hungarian diploid Scilla taxa (KERESZTY, original) — a. *Scilla vindobonensis* var. *vindobonensis;* b. *S. vindobonensis* var. *transdanubialis;* c. *S. vindobonensis* ssp. *borhidiana;* d. *S. kladnii*

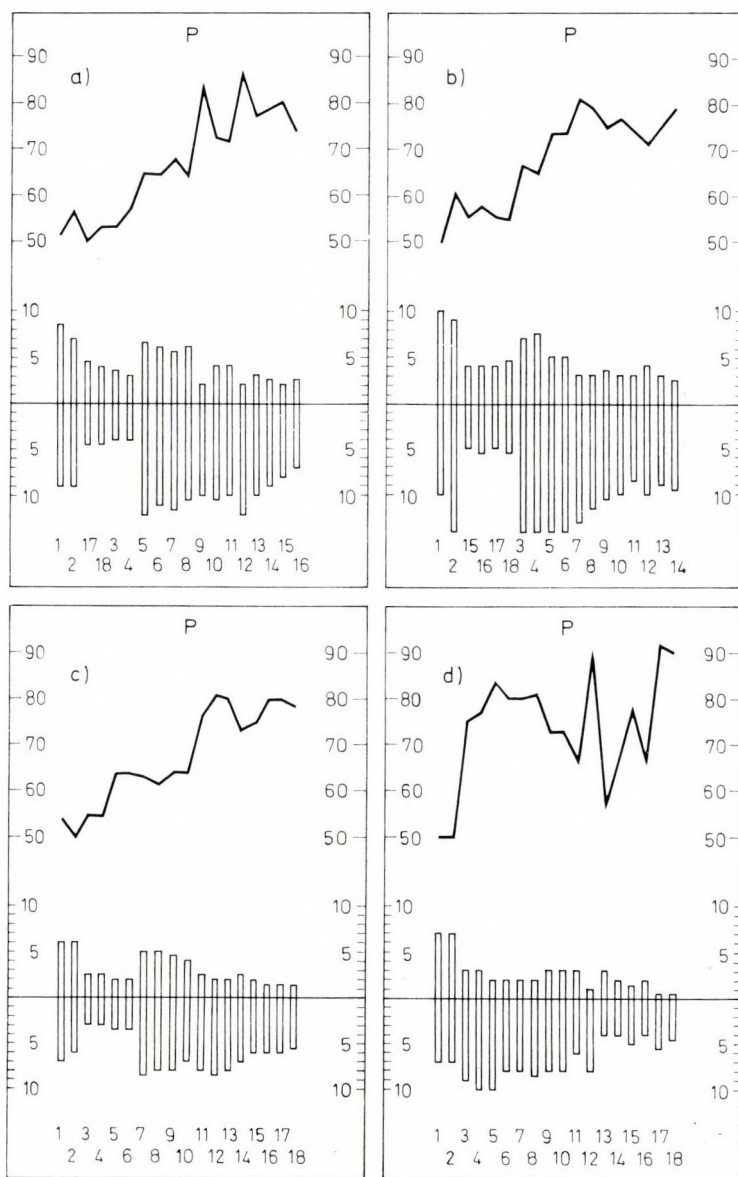



Fig. 3. CI–P curves of the Hungarian diploid *Scilla* taxa (KERESZTY, original). — For the abbreviations see Fig. 2

S. vindobonensis ssp. vindobonensis
S. vindobonensis ssp. vindobonensis var. transdanubialis
S. vindobonensis ssp. borhidiana
S. kladnii
S. drunensis ssp. buekkensis
S. drunensis ssp. drunensis
S. spetana
CI %
L^r

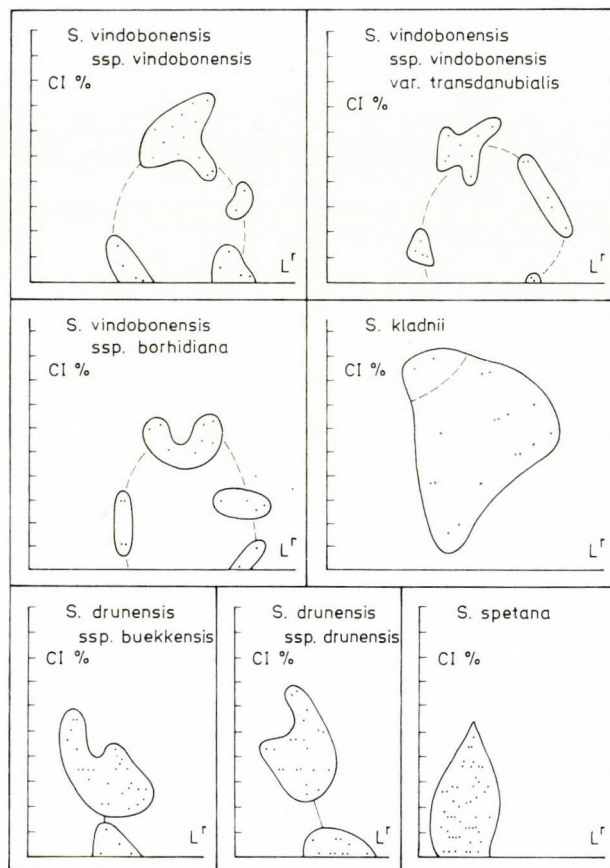



Fig. 4. Polykariograms of the Hungarian *Scilla* taxa (KERESZTY, original)

vindobonensis type is most similar to that of var. ***transdanubialis***. The curve of ssp. ***borhidiana*** is more different, whereas the curve of *S.* ***kladnii*** is even more distinct.

The polykaryograms of the studied taxa (Fig. 4) are represented according to the method of PATAU (1960). On the vertical axis are the centromer-index values, and on the horizontal one the relative length values of the chromosomes are measured. The shape and configuration of the diagrams provide a very instructive picture about the close relations of the different taxa especially as to the similarity of the tetraploids.

Comparison of the C-Banding karyotypes of *S. bifolia* and three *S.* ***vindobonensis*** taxa clearly shows the great difference and that the members of the ***vindobonensis*** group are fundamentally similar in basic structure (Fig. 5). The similarity of C-Banding patterns of the diploid *S.* ***bifolia*** and the tetraploid *S.* ***drunensis*** is doubtless (Fig. 6). It proves that the tetraploid taxa

Fig. 5. C-Banding patterns of some diploid *Scilla* taxa (after GREILHUBER 1978)

occurring in Hungary are closely related to the diploid *S. bifolia* which has not been found in Hungary.

As to the quantity of DNA in the chromosomes of the different taxa, GREILHUBER concluded that changes in the quantity of DNA within the genus were nearly always accompanied by taxonomic differences though sometimes only by very small morphological ones (GREILHUBER 1979). Our results confirm that the Hungarian *S. bifolia* s. l. populations represent several taxonomic units, separated from each other in geographical distribution as well.

Table 2 shows the DNA content and summarizes the statistical evaluation of the taxa. The significant separation of the great groups and an increased division of the tetraploids seem unambiguous. The taxonomic status of the

Table 2

DNA *content of Hungarian* Scilla Taxa

Taxon	N° of population	1 C_x L_n sL_n	N° of sample	ANOVA within taxa	ANOVA among taxa	ANOVA among groups
S. vindobonensis	1	9.32+−0.80	30	n = 100		
var. *vindobonensis*	2	9.52+−0.40	40	9.40+−0.528 Ø		
	3	9.30+−0.25	30	F = 1.749		
				p = 0.1793		
— var. *transdanubialis*	4	9.60+−0.25	20	n = 80	n 240	
	5	9.43+−0.54	30	F = 1.174	9.45+−0.61	
				p = 0.3155	F = 2.1038	
	6	9.65+−0.60	30	9.573+−0.51 Ø	p = 0.1244	
— ssp. *borhidiana*	7	9.63+−0.79	30	n = 60		n = 1089
	8	9.42+−0.78	30	9.39+−0.789 Ø	Ø	
				F = 0.0876		
				p = 0.7683		
S. *kladnii*	9	8.79+−0.69	100	n = 160		6.973+−2.02
				9.75+−0.618 Ø		
	10	8.75+−0.44	30	F = 0.8726 Ø		
	11	8.62+−0.50	30	p = 0.4199		
S. *drunensis*	12	5.74+−0.36	30	n = 180		
	13	5.80+−0.36	30	5.706+−0.303	n = 350	F = 4456.41
	14	5.82+−0.25	20	Ø	5.7+−0.312	
	15	5.68+−0.20	50	F = 3.002		
	16	5.61+−0.31	50	p = 0.020	F = 0.1077	$p < 0.00001$
S. *drunensis*	17	5.66+−0.37	30	n = 190	p = 0.7429	
ssp. *buekkensis*	18	5.68+−0.31	30	5.695+−0.32		
	19	5.68+−0.40	30	Ø	Ø	
	20	5.65+−0.28	50	F = 1.2069		
	21	5.78+−0.30	50	p = 0.3094		
S. *bifolia* s. str.	S.	5.80+−0.26	50	m = 106; W = 0.4054		
(S = Stopfenräuth, Au	F.	5.76+−0.37	56	5.77+−0.322		
F = S. G. in Fiore, It)				p = 0.5257 Ø		
S. *spetana*	K.	5.01+−0.24	153	n = 213; F = 2.1734		
(K = Kreuttal, Au)	22	5.06+−0.17	60	5.02+−0.22		
				p = 0.1419		

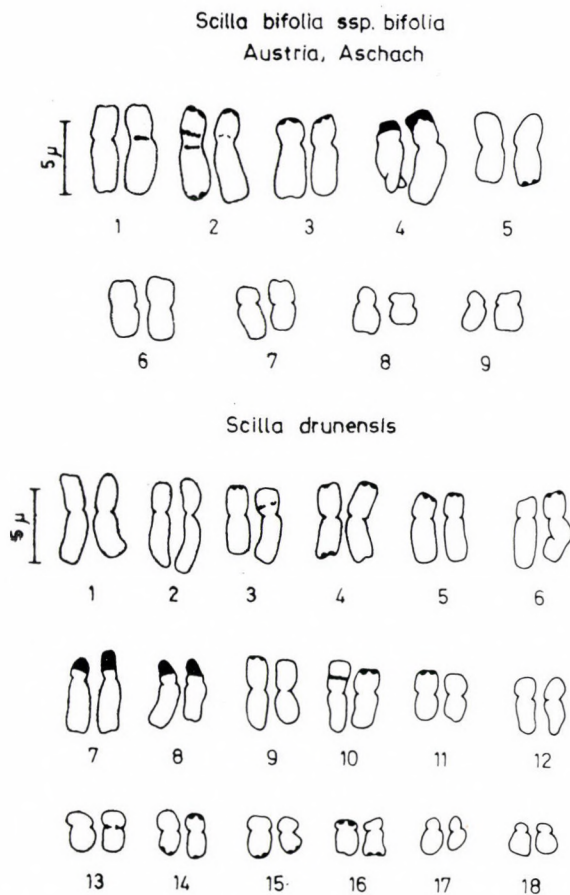
Scilla bifolia ssp. bifolia
Austria, Aschach

Scilla drunensis

Fig. 6. C-Banding patterns of *Scilla bifolia* s. str. and *S. drunensis* (after GREILHUBER 1978)

taxa in Fig. 7 is even more emphasized. Each column represents the DNA values in picogram calculated to the basic chromosome numbers. In addition to the morphological similarity the insignificant cytotaxonomical difference between the tetraploids also suggests that the two tetraploid taxa should be considered as subspecies rather than separate species as they are described (SPETA 1976). The single hexaploid population in the country can be separate from the others at species level considering the taxonomic importance of a small change and the specific stability of DNA content in this species (cf. GREILHUBER 1979).

The cytotaxonomic results supperted by morphological and biostatistical examinations have provided proof for the geographical separation of the ploidy levels of the populations in Hungary, confirming thereby the earlier view concerning their relict characteristics. The taxonomic importance of the

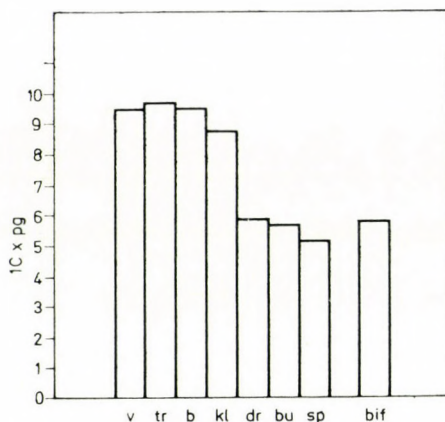



Fig. 7. The DNA-content of the studied *Scilla* taxa (after the data of GREILHUBER 1978 and GREILHUBER and KERESZTY 1988) — For the abbreviations see Fig. 1.; bif = S. bifolia

differences in DNA content suggests that the earlier species concept in this group needs revision.

On the basis of the results, the distribution of populations in Hungary is summarized in Fig. 8.

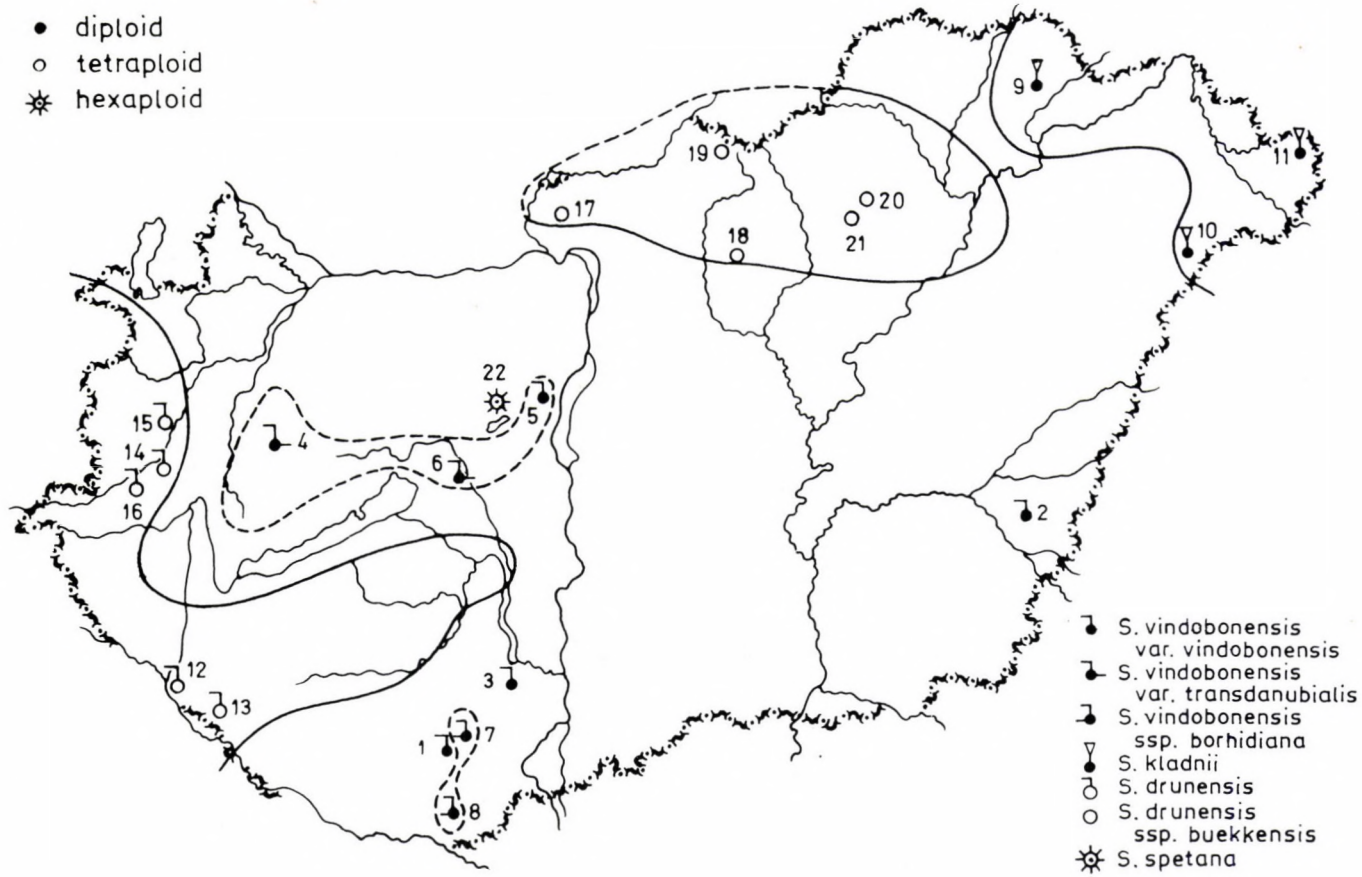
ACKNOWLEDGEMENTS

The author is indebted to Prof. G. VIDA and Dr. T. PUSZTAI for the critical reading of the text and to Prof. A. BORHIDI and Dr. J. PODANI for the revision of the English version of the article.

⟶

Fig. 8. The geographic distribution of the Hungarian *Scilla* populations studied for karyometry and DNA-content (see Table 2)

Localities:

1 Pécs, Baranya com. Éger-valley
2 Doboz, Békés com. Vargahossza-forest
3 Szekszárd, Tolna com. Sötét-valley
4 Bakonypölöske, Veszprém com. Kupi-forest
5 Érd, Pest com. Hamzsabégi-forest
6 Soponya, Fejér com. Fácános-forest
7 Pécs, Baranya com. Mt. Tubes
8 Nagyharsány, Baranya com. Mt. Szársomlyó
9 Makkoshotyka, Borsod com. Völgy-patak-valley
10 Nyírbátor, Szabolcs com. Bátorliget
11 Marosliget, Szabolcs com. Cserköz-forest
12 Belezna, Somogy com. Légrádi-hill
13 Berzence, Somogy com. Park-forest
14 Nagymákfa, Vas com. Hollósi-forest
15 Ikervár, Vas com. Ikervári-forest
16 Alsóújlak, Vas com. Kislyuk-forest
17 Nagybörzsöny, Pest com. Mt. Nagy-hideghegy
18 Mátraháza, Heves com. Mt. Sárhegy
19 Somoskőújfalu, Nógrád com. Mt. Karancs
20 Répáshuta, Borsod com. Mt. Kerekhegy
21 Cserépfalu, Borsod com. Hór-valley
22 Nadap, Fejér com. Mt. Templomhegy

REFERENCES

Borhidi, A. 1985: Taxonomic problems of the *Scilla bifolia* and *Molinia coerulea* complexes in Hungary. — Biosystematic Conference on the Northern European Flora, Stockholm, 26–28. Aug. 1985. Abstracts p. 21.

Greilhuber, J. 1978: DNA Contents, Giemsa Banding and Systematics in *Scilla bifolia*, *S. drunensis* and *S. vindobonensis* (Liliaceae). — *Pl. Syst. Evol.* **130:** 223–233.

Greilhuber, J. 1979: Evolutionary changes of DNA and heterochromatin amounts in the *Scilla bifolia* group (Liliaceae). — *Pl. Syst. Evol. Suppl.* **2:** 266–280.

Greilhuber, J., Kereszty, Z. 1988: Taxonomic significance of genome size and heterochromatin banding patterns in the *Scilla bifolia* alliance (Hyacinthaceae) in Hungary. — *Pl. Syst. Evol.* **140:** in press.

Greilhuber, J., Speta, F. 1977: Giemsa karyotypes and their evolutionary significance in *Scilla bifolia*, *S. drunensis* and *S. vindobonensis.* — *Pl. Syst. Evol.* **127:** 171–190.

Kereszty, Z. 1987: A hazai Scilla bifolia s.l. fajcsoport taxonómiai felülvizsgálata. (Taxonomic revision of the Scilla bifolia s.l. aggregate.) Diss. Cand. Sc. Manuscript. Budapest. Hung. Acad. Sci.

Kereszty, Z. 1987a: A magyarországi *Scilla bifolia* alakkör rendszertani felülvizsgálata II. Numerikus taxonómiai vizsgálatok. (Systematic revision of the Scilla bifolia group in Hungary II. Numerical studies.) — *Bot. Közl.* **74:** in press

Kereszty, Z. 1987b: A magyarországi *Scilla bifolia* fajcsoport taxonómiai értékelése. (Toxonomic evaluation of the Scilla bifolia aggregate in Hungary.) — *Bot. Közl.* **74:** in press.

Kereszty, Z., Szilágyi, L. 1986: Cytological investigation of *Scilla bifolia* Populations in Hungary II. — *Acta Bot. Hung.* **32:** 167–176.

Kereszty, Z., Szilágyi, L., Borhidi, A. 1986: Biosystematic studies of the *Scilla bifolia* complex in Hungary. — *Acta Univ. Ups. Symb. Bot. Ups.* **XXVII/2:** 107–112.

Patau, K. 1960: The identification of individual chromosomes, especially in man. — *J. Human Genetics* **12:** 285.

Speta, F. 1977: Cytotaxonomischer Beitrag zur Kenntnis der Scilla Arten Ungarns und Siebenbürgens. — *Naturk. Jahrb. Stadt Linz* **22:** 9–63.

Acta Botanica Hungarica 33 (3–4), pp. 317–324 (1987)

SUPPLEMENTARY INVESTIGATIONS INTO THE RANGE OF RELATION OF ANGIOSPERMOUS SPECIES ON THE BASIS OF THE PROLINE CONCENTRATION OF POLLEN

G. PÁLFI[1] and S. GULYÁS[2]

DEPARTMENT OF PLANT PHYSIOLOGY[1] AND BOTANY[2], ATTILA JÓZSEF UNIVERSITY, SZEGED, HUNGARY 6701. P. O. Box 657

(Received: 28 October 1985)

We examined 65 plant species for the free proline concentration of the pollen at the time of pollination. In 49 species the proline content made 1.0–2.5 per cent of the dry matter. They were given the name proline type pollen. In 16 species the proline concentration did not exceed 0.3 per cent (non-proline type pollen). We found that they way of pollination, that is the fact that the species was autogamous entomophilous, and anemophilous plant did not influence the extent of proline accumulation. In the course of studies on species from 30 families of different development stage in the di- and monocotyledonous classes of Angiosperms it came to light that the proline type of the pollen was not in connection with these stages of phylogeny. The proline-accumulating capacity of the pollen may be quite different in the species of a family. We detected 6 families in which the pollens of some species were proline type while those of other species were non-proline type. The species of the genera, on the other hand, showed complete uniformity as for the extent of proline accumulation. Thus, the proline type of the pollen can be a chemotaxonomic character mainly in a narrower range of relation.

Introduction

STANLEY and LINSKENS (1974), BRITIKOV (1985) and DASHEK and MILLS (1981) pointed out that the proline, one of the free amino acids, showed a positive correlation with the vitality and fertility of pollens. The proline concentration of pollens in itself is higher than the total concentration of all the other protein amino acids, and may even reach 1.5–2.5 per cent of the dry matter of pollens (TUPÝ 1963, AHOKAS 1968, KURSAKOV and RYZHKOV 1980, ZHANG et al. 1982). According to the authors there is a close relation between the proline concentration and fertility level of pollen grains.

The proline has been found to play an important role in the energetic transformation of the germinating pollen and in the interactions with the style. Besides the proline is an efficient activator of the KREBS cycle and controls the water balance of the pollen and the activity of certain enzymes (DASHEK and HARWOOD 1974, LIRSKENS 1974, ALARKON et al. 1978, HESLOP-HARRISON 1979, ZHANG et al. 1982). Other authors add that the role of proline is particularly important in the synthesis of glycoproteins that are rich in hydroxy-proline and indispensable during the elongation of the cell-wall and of the wall of the pollen tube (TUPÝ 1963, STANLEY and LINSKENS 1974, BRITIKOV 1975, AHOKAS 1978, KURSAKOV and RYZHKOV 1980, DASHEK and MILLS 1981).

The influence of proline on the vitality of pollens is due among others to their higher concentration whereby it increases their drought- and cold resistance to a considerable extent (PÁLFI et al. 1981, ZHANG et al. 1982, ZHANG and CROES 1983, PÁLFI and KÖVES 1984). According to the latter authors the correlation found between the proline content and vitality and/or fertility of pollens can be pointed out in numerous plant species.

In our present paper we try to give answer to the question what, in general, the proline concentration is at which this amino acid determines the optimum level of vitality, and in what species it is realized. Further questions to be answered are: whether the proline accumulation of the pollen is a characteristic of species, genus or family; whether the extent of proline accumulation in the pollen can be used in the chemotaxonomy of species. We try to clear up whether the way of pollination (autogamy, entomophily and anemophily) and the stage of phylogeny are related with the concentration of proline.

Pálfi et al. (1981) and Pálfi and Köves (1984) made amino acid extracts from pollen masses of 18 inbred maize lines and 6 maize hybrids. They found that pollens with higher proline concentrations possessed a higher degree of vitality. Further, among a number of improved rye varieties belonging to the same species the one with a higher proline concentration showed the higher in vitro germination percentage.

We already published our new quick staining method based on the proline concentration by which the degree of pollen vitality can be determined grain by grain (Pálfi and Köves 1984). In our present work the vitality of pollen in some angiospermous species is demonstrated through their amino acid extracts and the positive or negative result of isatin staining, too.

Material and methods

The names of the collected and examined families and species are given in tables. The anthers of insect-pollinated species were dissected in laboratory then fixed at 90 °C and dried. Pollen grains thus preserved can be stained either immediately, or even 1–2 years later since the concentration of proline no longer changes (Stanley and Linskens 1974). The composition of the isatin reagent is: 0.6 ml crystalline acetic acid added to 20 ml acetone, and 0.20 g isatin dissolved in it.

Staining is carried out in the following way: a 2–5 mg mass of pollen is placed onto a microscope slide, 1 or 2 drops of the isatin reagent are added to it, the pollen grains are thoroughly mixed with the stain until the solvent evaporates. The reagent is added twice to the pollen, one drop on each occasion, and the solvent is evaporated while it is stirred. Then the preparation is placed for 12 minutes in a thermostat heated to 90 °C to react. When the preparation has cooled down 1 drop of paraffine oil is added to the mass of pollen stuck on, thororughly mixed with it, then a cover glass is placed on the preparation.

Staining is evaluated by light microscope magnified 50–300 times. The proline content in the amino acid extracts made from the pollen masses (10–20 mg) was measured by the method of Aspinall et al. (1973) in 3 replications.

Results and Discussion

As the concentration of proline increases in them the pollen grains are stained first dark greenish blue, then dark blue and black. This is the positive isatin staining that characterizes the vital pollen grains. Pollen grains without vitality retain their original yellow colour or strain light brown (negative isatin reaction).

However, in black-and-white photoes taken by microscope such colours are not obtained; here the black indicates the vital pollen grains while the different shades of grey point to those without vitality (Plate I).

In photoes 1–12. of Plate I. vital pollen grains stained black mostly are seen mixed with non-vital ones showing various shades of grey. The pictures show but a small part of the visual field of the microscope. The actual enlargement used enables us to study the colour for 120–150 pollen grains. With the pollen colours of 5 such visual fields evaluated and the results averaged an approximate percentage value of the vitality can be obtained.

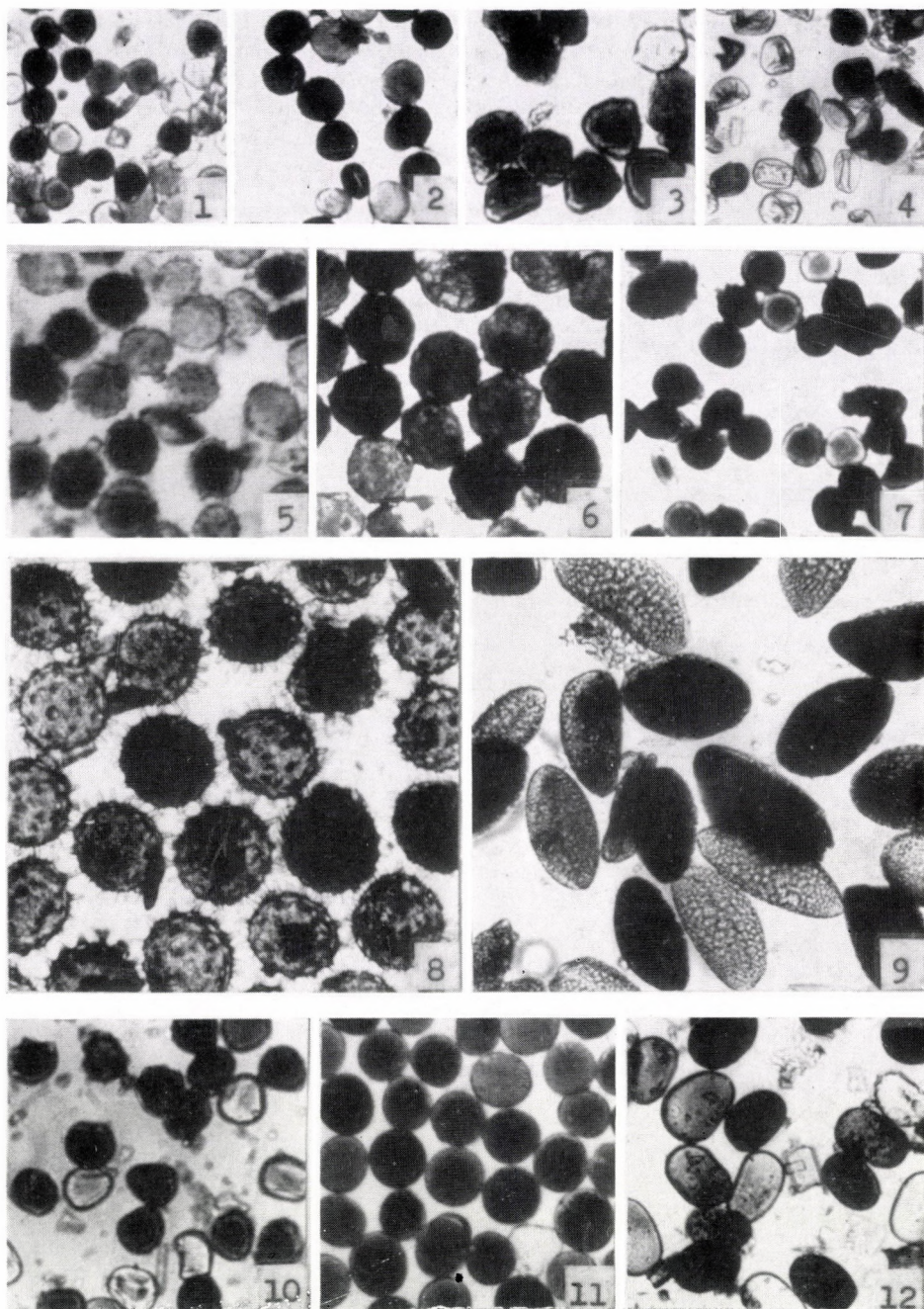



Plate I

Staining pollen grains with isatin reagent. Pollen grains stained black are vital (positive isatin reaction.) Pollen grains not stained (grey) did not possess vitality. 1 = *Papaver somniferum*; 2 = *Linum austriacum*; 3 = *Malus pumila*; 4 = *Robinia hispida*; 5 = *Chrysanthemum hortorum*; 6 = *Opuntia vulgaris*; 7 = *Digitalis lanata*; 8 = *Hibiscus rosa-sinensis*; 9 = *Hemerocallis fulva*; 10 = *Hordeum vulgare*; 11 = *Zea mays*; 12 = *Secale cereale*. (Magnified 100–300 ×)

Most so far known methods used to point out vitality and/or fertility are mainly based on the percentage of pollen grains viable or germinable at the beginning of the examination. The success of the isatin reaction, on the other hand, does not depend at all on the fact whether the pollen grains to be studied are viable or fixed. This is a great advantage of the isatin method.

Parallel with the isatin reaction values the proline concentrations of pollen extracts are also given in the tables.

Table 1

Proline concentrations of amino acid extracts from pollen grains of entomophilous, anemophilus and autogamous plant species as percentages of dry matter, and the positive reaction of pollen grains to isatin reagent, that is the percentage of pollen grains stained black (vitality). Dicotyledons, 17 families

Families	Species	Proline concentration of pollens	Positiv reaction with isatin
		%	
Ranunculaceae	1. *Clematis vitalba*	1.56	58
Nymphaeaceae	2. *Nymphaea alba*	1.26	50
Rosaceae	3. *Malus pumila*	1.55	65
Grossulariaceae	4. *Ribes aureum*	1.27	49
	5. *R. rubrum*	1.34	52
Fabaceae	6. *Trifolium repens*	1.57	64
	7. *T. pratense*	1.47	57
	8. *Robinia hispida*	1.44	56
	9. *R. pseudo-acacia*	1.36	55
Tiliaceae	10. *Tilia cordata*	2.11	89
	11. *T. platyphyllos*	1.88	85
Malvaceae	12. *Abutilon theophrasti*	1.51	63
	13. *Hibiscus rosa-sinensis*	1.18	45
Solanaceae	14. *Solanum nigrum*	2.24	92
	15. *S. tuberosum*	2.31	94
	16. *S. melongena*	1.92	87
	17. *Datura inoxia*	2.18	91
	18. *D. arborea*	2.06	87
Papaveraceae	19. *Papaver rhoeas*	2.15	88
	20. *P. somniferum*	1.53	62
Cruciferae	21. *Lepidium draba*	1.27	46
Cucurbitaceae	22. *Cucumis sativus*	1.54	62
Compositae	23. *Bellis perennis*	1.38	56
	24. *Chrysanthemum hortorum*	1.83	84
	25. *C. leucanthemum*	1.75	80
Primulaceae	26. *Primula veris*	2.24	94
	27. *P. acaulis*	2.31	95
Betulaceae	28. *Betula pendula*	1.25	46
	29. *Corylus avellana*	2.18	89
	30. *Alnus glutinosa*	1.12	40
Fagaceae	31. *Quercus robur*	1.27	46
Juglandaceae	32. *Juglans regia*	1.45	56
Salicaceae	33. *Salix babylonica*	2.06	88
	34. *S. smithiana*	2.15	90
	35. *S. cinerea*	2.18	91
	36. *Populus tremula*	1.23	43
	37. *P. alba*	1.20	41

(Average deviation below $\pm$ 5 per cent; n = 5 and 3)

Table 2

Proline concentrations of pollen extracts from monocotyledonous species, and positive isatin reactions of pollen grains (vitality percentages). Entomophilous, anemophilous and autogamous species

Families	Species	Proline concentration of pollens	Positiv reaction with isatin
		%	
Liliaceae	1. *Colchicum autumnale*	1.82	81
	2. *Hemerocallis fulva*	1.51	60
	3. *Allium schoenoprasum*	1.38	53
	4. *Lilium candidum*	1.17	42
	5. *L. martagon*	1.20	43
	6. *Muscari comocum*	1.24	44
Iridaceae	7. *Iris pumila*	1.52	60
	8. *I. germanica*	1.53	62
Gramineae	9. *Secale cereale*	1.25	50
	10. *Triticum aestivum*	1.68	74
	11. *Hordeum vulgare*	1.72	76
	12. *Zea mays*	2.46	96

(Average deviation below $\pm$ 5 per cent: n = 5 and 3)

In Table 1 37 dicotyledonous species of 17 families are contained. The serial numbers of species more or less follow the order of phylogenetic development. Insect- and wind-pollinated species are found mixed in the table.

As seen from Table 1 the proline concentrations of extracts made from the pollen masses were higher than 1.0 per cent for all 37 species, and in the case of 12 species they even exceeded 2.0 per cent. At the same time, the vitality percentages obtained by the isatin method ranged from 40 to 95 per cent.

Furthermore, the data of Table 1 show that the vitality percentages determined by isatin staining generally rise in proportion to the prolin concentrations of the amino acid extracts, which suggests that the level of vitality is really in connection with the proline concentration of the pollen, and in a linear connection. This fact was confirmed by the results of in vitro germination obtained with the pollen of inbred maize lines in agar medium (Pálfi and Köves 1984). The results obtained with the highest plants, i.e. with monocotyledonous species, are shown in Table 2.

In Table 2 proline- and positive isatin reaction data for 12 (insect-, wind- and self-pollinated) species from 3 families are seen. The proline concentrations in the pollen extracts of the species fall between 1.17 and 2.46 per cent. As seen from the table the species showing the lowest proline concentration gave the lowest positive isatin reaction again *(Lilium candidum)*, and the highest vitality percentage determined by the isatin method was, in turn, pointed out for the species with the highest proline concentration in the pollen *(Zea mays)*. Thus, between the monocotyledonous and dicotyledonous species, that is in the two kinds of data included in Tables 1 and 2 and in their proportions compared to each other there are no differences.

In the plant species listed in Table 3 the proline concentrations of extracts from mature pollen grains ate not high. The table contains 16 di- and monocotyledonous species of 10 families in which the proline concentrations of the pollen are quite low (ranging between 0.12 and 0.28 per cent). In the case of such low proline concentrations the isatin reaction is negative,

Table 3

Dicotyledonous and monocotyledonous species with quite low proline concentrations of pollen grains and consequent negative isatin reactions. Entomophilous species of 10 families

Families	Species	Proline concentration of pollens	Positiv reaction with isatin
		%	
Fabaceae	1. *Coronilla varia*	0.20	—
Malvaceae	2. *Lavathera thuringiaca*	0.27	—
Labiateae	3. *Ajuga genevensis*	0.28	—
	4. *Lamium purpureum*	0.22	—
	5. *Glechoma hederacum*	0.18	—
Cruciferae	6. *Brassica napus*	0.26	—
	7. *Arabis procurrens*	0.15	—
Tamaricaceae	8. *Tamarix tetrandra*	0.12	—
Begoniaceae	9. *Begonia semperflorens*	0.23	—
Cucurbitaceae	10. *Cucurbita pepo*	0.17	—
	11. *C. ficifolia*	0.21	—
	12. *C. maxima*	0.20	—
Compositae	13. *Helianthus annuus*	0.23	—
Liliaceae	14. *Tulipa germanica* gelb	0.18	—
	15. *T. gesneria* rot	0.23	—
Amaryllidaceae	16. *Narcissus pseudonarcissus*	0.28	—

(Average deviation below $\pm$ per cent: n = 5 and 3)

that is, none of the pollen grains are stained dark blue or black. Consequently, the isatin method cannot be used to determine the vitality for the 16 species of Table 3. Among the species in Table 3. those at lower and higher stages of phylogeny are equally found.

Taking the present and earlier published (Pálfi 1982, Pálfi and Köves 1984) proline concentration data of pollen into consideration we attempted to set up an artificial proline threshold by means of which the species can be divided in two groups: group 1: "proline type species" in which the proline concentration of mature and vital pollen grains reaches 1.0 per cent of the dry matter; group 2: "non-proline type species". The proline concentration of vital pollen grains in the species of group 2 is below 1.0 per cent (in most cases the proline is ten times less than in the species of group 1).

Evaluating the data of the species included in Tables 1, 2 and 3 we find that 49 of the species examined can be placed among the proline type- and 16 among the non-proline type species. Accordingly, we detected three times more proline type- than non-proline type species. Determining the vitality on the basis of the positive isatin reactions of pollen grains is a promising method.

According to the data of the tables the proline type of the pollen does not seem to be a family character, since we found 6 families that included both proline type and non-proline type species (Fabaceae, Malvaceae, Cruciferae, Cucurbitaceae, Compositae, Liliaceae). This also means that the genera within a family represent different development stages. On the other hand,

the species belonging to the same genus are in each case either of proline type (Table 1: *Ribes, Trifolium, Robinia, Tilia, Solanum, Datura, Papaver, Chrysanthemum, Primula, Salix, Polulus;* Table 2: *Lilium, Iris*) or not (Table 3: *Cucurbita, Tulipa*).

Thus, according to proline type the genera show uniformity or close relationship. Hence it is supposed that this characteristic can be used in chemotaxonomy. This, however, requires studying numerous further families and species.

In Tables 1 and 2 autogamous, entomophilous and anemophilous species are equally found, which proves that the way of pollination is in no connection with the proline type of the pollen.

According to our data the proline concentration of the pollen in the proline type plant species generally falls within 2.0 and 2.5 per cent, at which the vitality of the pollen grains is optimum. In the case of a proline content of 1.0–1.5 per cent a 40–60 per cent vitality of pollen can be expected. It can be supposed that the optimum proline concentration of pollen grains in the individual species show some differences. In order to obtain a totally exact result the pollen of every cultivated species is worth being studied in detail. In our previous works we determined the degree of vitality for many inbred lines, hybrids and varieties of maize and rye by the isatin method (PÁLFI et al. 1981, PÁLFI 1982, PÁLFI and KÖVES 1984). KURSAKOV and RYZHKOV (1980) demonstrated on the pollen grains of *Ribes nigrum* when proline was added to the in vitro germination medium the elongation of pollen tubes increased by 100 per cent compared to the proline-free control. We obtained similar results in experiments with the pollen grains of *Zea mays* (PÁLFI and KÖVES 1984), which suggests that a large amount of proline ensures advantages in the course of pollen germination. These advantages are described in detail by LEVITT (1980), and PALEG and ASPINALL (1981).

REFERENCES

Ahokas, H. 1978: Cytoplasmic male sterility barley. II. Physiology and anther cytology of msml. *Hereditas* **89:** 7–21.

Alarkon, N. L., Larionova, N. A., Minina, E. G., Mitrofanova, T. K., Tolkachev, O. N. 1978: Aminokisloti pilchi kedra sibirskogo. *Fiziol. Rasteniy.* **25:** 855–857.

Aspinall, D., Singh, T. N., Paleg, L. G. 1973: Stress metabolism V. Abscisic acid and nitrogen metagolism in barley and *Lolium temulentum* L. *Austral. J. Biol. Sci.* **26:** 319–327.

Britikov, E. A. 1975: *Biologicheskaya Roly Prolina.* Izd. Nauka Moscow, 36–44.

Dashek, W. V., Harwood, H. I. 1974: Hydroxyproline and lily pollen tube elongation. *Ann. Bot.* **38:** 947–959.

Dashek, W. V., Mills, R. R. 1981: Proline metabolism by germinating *Lilium longiflorum.* I. Labelling of cytoplsmic wall and culture medium molecules. *Acta. Soc. Bot. Pol.* **50:** 51–66.

Heslop-Harrison, J. 1979: Aspects of structure, cytochemistry and germination of the pollen of rye (*Secale cereale*). *Ann. Bot.* London. **44.** Suppl. 1–47.

Kursakov, A. B., Ryzhkov, S. D. 1980: Soderzhanie svobodnih aminokislot v raznoimeno zaryazhennih frakciyah pilchi chernoy smorodini. *Fiziol. Rasteniy.* **27:** 735–739.

Levitt, J. 1980: *Responses of Plants to Environmental Stresses.* Vol. II. Water, Radiation, Salt, and Other Stresses. Academic Press. New York, London, Toronto, Sydney, San Francisco. 58–143.

Linskens, H. F. 1974: *Fertilization in Higher Plants.* North-Holland Publ. Co, Amsterdam. 137–143.

Paleg, L. G., Aspinall, D. 1981: *The Physiology and Biochemistry of Drought Resistance in Plants.* Academic Press. Sydney, New York, London, Toronto, San Francisco. 206–231.

Pálfi, G., Köves, E. 1984: Determination of vitality of pollen on the basis of its amino acid content. *Biochem. Physiol. Pflanzen.* **179:** 237–240.

Pálfi, G., Pálfi, Zs. 1982: A rapid method for the determination of fertility of maize pollen with the proline-isatin reaction. *Maydica.* **27:** 107–111.

Pálfi, G., Pintér, L., Pálfi, Zs. 1981: The proline content and fertility of the pollen of inbred maize lines. *Acta Bot. Acad. Sci. Hung.* **27:** 179–187.

Stanley, R. G., Linskens, H. F. 1974: *Pollen Biology, Biochemistry, Management.* Springer Verlag. Berlin Heidelberg New York. 154–159.

Tupý, J. 1963: Free amino acids in apple pollen from the point of view of its fertility. *Biol. Plantarum.* **5:** 154–159.

Zhang, H. Q., Croes, A. F. 1983: Proline metabolism in pollen: degradation of proline during germination and early tube growth. *Planta.* **159:** 46–49.

Zhang, H. Q., Croes, A. F., Linskens, H. F. 1982: Protein synthesis in germinating pollen of *Petunia:* role of proline. *Planta.* **154:** 199–202.

Acta Botanica Hungarica 33 (3—4), pp. 325—331 (1987)

XYLOTOMIC STUDY OF SOME VENEZUELAN SPECIES OF THE CAPPARACEAE II.

K. BABOS[1], I. R. BERMUDEZ[2] and L. J. C. CUMANA[2]

[1] RESEARCH INSTITUTE FOR WOOD INDUSTRY, BUDAPEST, HUNGARY
[2] BIOLOGICAL DEPARTMENT OF SCIENTIFIC SCHOOL, UNIVERSITY OF ORIENTE, CUMANA, VENEZUELA

(Received: 10 May 1986)

The authors describe the external morphological features, ecological conditions, occurrence, and major anatomical characteristics of the xylem for two woody species of the family Capparaceae from Venezuela: *Morisonia americana* L. and *Crataeva tapia* L.

Materials and methods

Blocks of the two species were softened in a 1 : 1 ratio mixture of water and glycerine at 1.5–2.0 atm. in a J. BRINZER autoclave, then cross-, radial- and tangential sections were prepared from them. The sections were dyed in an alcoholic solution of the microdyestuff of toluidine blue. Maceration of the tissues was performed by SCUHLZE's method (SÁRKÁNY—SZALAI 1964).

Lengths of the fibres and vessel elements, tangential and radial diameters of the vessels, widths and heights and other characteristics of the medullary rays were measured. Minimum-, average- and maximum values were calculated from 50–100 measurements for each anatomical feature of the species.

Of the sections suitably enlarged microphotographs were made.

Exterior morphology and occurrence

Morisonia americana L.

Shrub or tree, 2–4 m in height (Fig. 1). Bark covered by shiny hair when young. Leaves simple, alternately set, reticulate-veined; leaf-blade 8.5–34 cm long, oblong-elliptic or oblong-lanceolate, obtuse at the base, acute at the apex, subentire, margin undulate. Inflorescence cauliflorous, racemose or single, 3–8 cm long (Fig. 2); flowers in racemes 2.5–2.8 cm long, hermaphrodite and actinomorphous. Calyx with 2–3 sepals, sepals 0.5–1 cm long, covered by shiny hairs; petals 4, opposed, stiff and yellow, 0.5–1.8 cm long. Stamina 25–26, 1.3–1.5 cm long, anthers 2–5 mm long, oblong, yellow, dehiscence longitudinal. Ovary 4–6 mm long, yellow, bicarpelar, one-celled with two pseudosepta, multiovulate, ovules with basal-lateral placentation; style 4–7 mm long. Berry, 3.5–7 cm, yellow or light chestnut, attached by a pedicel to the branch or trunk.

Fig. 1. Morisonia americana L., shrub, picture of habitus. (Photo: L. G. GONZALES)

Fig. 2. Cauliflorous flower of *Morisonia americana* L. (Photo: L. G. GONZALES)

Fig. 3. Crataeva tapia L., tree, picture of habitus. (Photo: L. G. GONZALEZ)

Fig. 4. Crataeva tapia L., foliage and berries. (Photo: L. G. GONZALEZ)

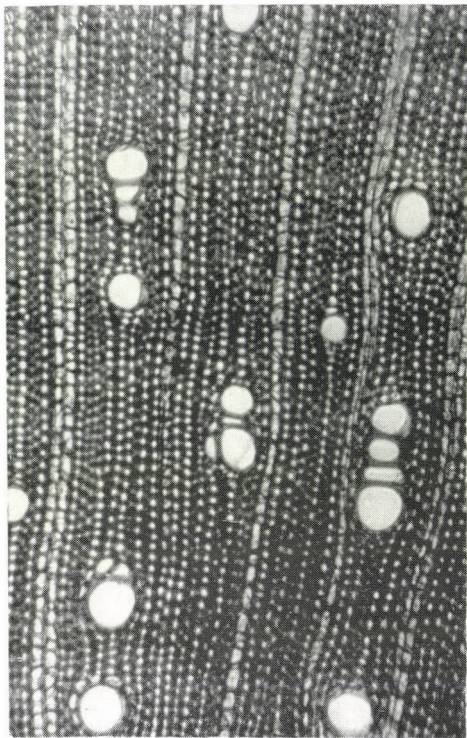



Fig. 5. Morisonia americana L. Cross section 120× Tracheae, trachea groups, medullary rays and fibres. Contact vasicentric longitudinal parenchyma

Fig. 6. Morisonia americana L. Tangential longitudinal section 120× One-, two- and three-cell wide medullary rays, thin-walled fibres. Trachea with alternating bordered pits

It lives on dry, gritty soils poor in nutrients, frequently along roads, scattered or in groups, in the provinces Falcón, Lara, Miranda, Nueva, Esparta, Sucre, Zulia and Otto of Venezuela.

Material studied was collected in El Tacal, 10. February 1983 by L. G. GONZALEZ and I. BERMUDEZ.

Crataeva tapia L.

Tree up to 5–8 m in height when old. (Fig. 3) Bark glabrous. Leaves compound, tripinnate, glabrous and shiny, alternately set; blade 3.5–15 cm long, oblong-elongate, reticulate-veined, obliquous or wedge-shaped at the base, long attenuate at the apex, entire. Flowers terminal, 7–8 cm long, hermaphrodite, partially zygomorphous, with 5–10 cm long pedicels. Sepals 4–6, 6–7 mm long, orbicular, greenish-yellow, covered by shiny hairs; corolla with 4–5 petals, petals 1.5–2.5 cm long, white, glabrous. Stamina 26–64, 4–5 cm long, anthers oblong, yellow. Ovary 3–5 mm long, superior, style 4.5–5 cm long; ovary uni- or bilocular with a pseudoseptum, glabrous, yellow, multiovulate; ovules with basal-lateral placentation. Berry glabrous, chestnut-coloured, attached with a 5–11–16.5 cm long pedicel to the branch (Fig. 4).

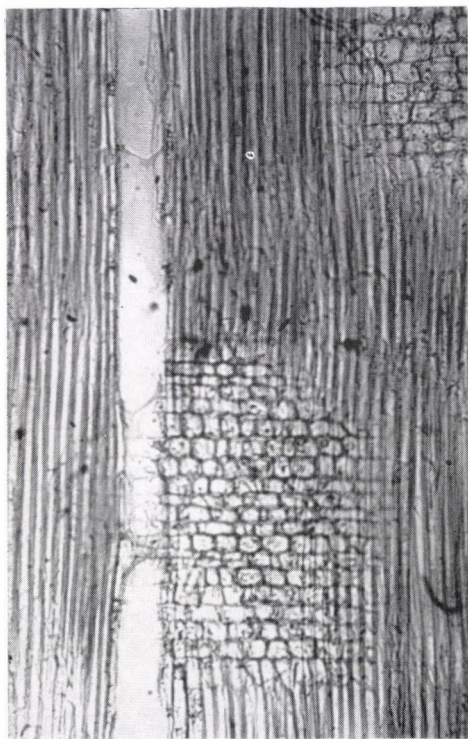



Fig. 7. Morisonia americana L. Radial longitudinal section 120 × Heterogeneous medullary rays, trachea, longitudinal parenchyma, fibres

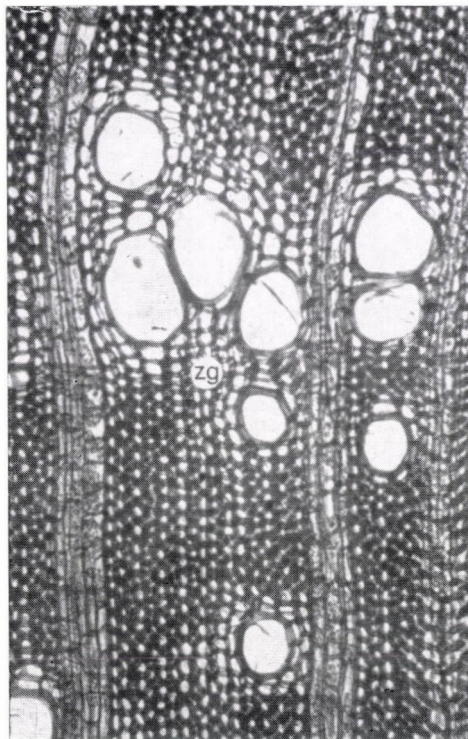



Fig. 8. Crataeva tapia L. Cross section 120 × Tracheae, trachea groups, wide medullary rays and fibres. Aliform-confluent longitudinal parenchyma
zg = zone of growth

It lives on dry, sandy and gritty soils poor in nutrients, generally singly, seldom in small stands, in the provinces Apure, Bolivar, Miranda, Sucre of Venezuela, and on areas along the river Amazonas.

Material studied was collected at Edo Sucre, 12. February 1983, by L. G. GONZALEZ and I. BERMUDEZ.

Wood anatomy

Morisonia americana L.

Wood porous diffuse; the ground mass of the wood is formed by polygonal-shaped fibres with thin wall and wide lumen. Contact vasicentric longitudinal parenchyma. Medullary rays with one to three cells in width (Fig. 5). The annual ring structure is not visible in the wood.

Tracheae are round or oval, in the groups (of 2–8) flattened in tangential direction. They are 18–33–56/mm² in number. Tangential diameter 27.9–41.6–60.4 μm. Radial diameter 27.9–46.8–65.1 μm. Vessel members are 37.2–189.8–330.1 μm long, with oblong bordered pits on the wall. The tracheae sometimes contain gum material. Perforation plate is simple.

Fig. 9. Crataeva tapia L. Tangential longitudinal section 120× Wide medullary rays, thin-walled fibres. Trachea with alternately set bordered pits on the wall

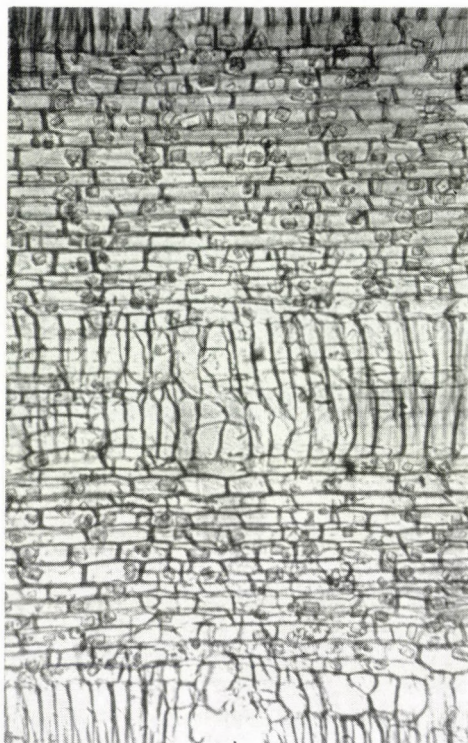



Fig. 10. Crataeva tapia L. Radial longitudinal section 120× High heterogeneous medullary eay, with square, oblong, diamond-shaped and amorphous calcium oxalate crystals in the cells

Medullary rays are rarely one-cell, more often 2–3 cells in width, with heterogeneous structure. Height 207.0–574.2–2070.0 μm. Width 11.5–31.7–46.0 μm (Figs 6–7)

Fibres are arranged in irregular and radial lines. Diameter 6.9–9.7–11.5 μm. Constant wall thickness 4.6 μm. Full length 426.0–582.1–853.0 μm. Tips of fibres commonly ending in a short smooth peak, sometimes one of them is tooth-edged.

Tangential diameter of the longitudinal parenchyma cells is 9.3–11.7–13.9 μm. Heigth 41.8–75.8–120.9 μm.

Crataeva tapia L.

Wood porous diffuse. The ground mass of the wood is formed by polygonal-shaped fibres with thin wall and wide lumen. Aliform-confluent longitudinal parenchyma. Medullary rays generally 3–6 cells, rarely one-cell in width. The annual ring structure is visible in the wood (Fig. 8).

Tracheae are round or oval, in the groups (of 2–3) flattened in tangential direction. They are 14–24.7–30/mm² in number. Tangential diameter 32.5–50.8–69.8 μm. Radial diameter 41.8–65.2–88.3 μm. Vessel members are 79.0–131.5–186.0 μm long, with alternating medium size bordered pits on the wall. Perforation plate is simple.

Table 1

Characteristics of the woody plant species studied

Elements	Features	*Morisonia americana*	*Crataeva tapia*
Trachea members	Arrangement	diffuse, solitary or groups of 2–8	diffuse, solitary or groups of 2–3
	Shape	round or oval	round or oval
	Tangential diameter	27.90–41.57–60.45 μm	32.55–50.78–69.75 μm
	Radial diameter	27.90–46.78–65.10 μm	41.85–65.19–88.35 μm
	Length of vessel members	37.2–189.8–330.1 μm	79.0–131.5–186.0 μm
	Number per sq mm	18.0–33.2–56.0	14.0–24.7–30.0
	Wall thickness	2.3–3.13–4.6 μm	4.6–5.93–6.9 μm
	Intervascular pitting	oblong, bordered	alternating, bordered
	Perforation plate	simple	simple
	Content	rarely mastic	—
Medullary rays	Width	wide	wide
	Number of cells	1–3	1–3–6
	Classification	heterogeneous	heterogeneous
	Height	207.0–574.2–2070.0 μm	149.5–460.69–793.5 μm
	Width	11.5–31.68–46.0 μm	57.5–81.88–115.0 μm
	Content	—	numerous calcium oxalate crystals
Fibres	Arrangement	irregular and in radial lines	irregular and in radial lines
	Shape	polygonal	polygonal
	Full diameter	6.9–9.7–11.5 μm	13.8–16.9–23.0 μm
	Wall thickness	constant 4.6 μm	constant 2.3 μm
	Full length	426.0–582.1–853.0 μm	355.0–585.7–923.0 μm
	Type of pitting	very small, slot-like	very small, cavernous
Longitudinal parenchyma	Arrangement	contact vasicentric	aliform-confluent
	Cell diameter, tang.	9.3–11.7–13.9 μm	9.3–17.4–23.2 μm
	Cell height, tang.	41.8–75.8–120.9 μm	46.5–126.6–195.3 μm
	Number of cells	2–3–4	1–2–4
	Content	—	—
	Other	—	—

Medullary rays are rarely one-cell, commonly 3–6-cell wide, with heterogeneous structure. Height 149.5–460.7–793.5 μm. Width 57.5–81.9–115.0 μm. Cells of medullary rays contain numerous square, oblong, diamond-shaped and amorphous calcium oxalate crystals (Figs 9–10).

Fibres are arranged in irregular and radial lines. Diameter 13.8–16.9–23.0 μm. Constant wall thickness 2.3 μm. Full length 355.0–585.7–923.0 μm. Tips of fibres commonly end in smooth short peaks, one of them sometimes bifurcates.

Tangential diameter of the longitudinal parenchyma cells is 9.3–17.4–23.2 μm. Height 46.5–126.6–195.3 μm.

For detailed anatomical characteristics of wood in the two species see Table 1.

REFERENCES

Metcalfe, C. R., Chalk, L. 1950: *Anatomy of the Dicotyledons.* – Vol. I. Clarendon Press. Oxford. pp. 91–93.

Sárkány, S., Szalai, I. 1964: *Növényszervezettani Gyakorlatok* (Plant Anatomy Practicum). — Tankönyvkiadó. Budapest. pp. 559.

Acta Botanica Hungarica 33 (3—4), pp. 333—351 (1987)

ANATOMÍA DE MADERAS DE CUBA. III

M. A. Vales[1], y Raquel Carreras[2]

[1] INSTITUTO DE BOTÁNICA. ACADEMIA DE CIENCIAS DE CUBA
[2] CENTRO DE INVESTIGACIÓN FORESTAL. MINISTERIO DE AGRICULTURA, CUBA

(Received: 10 October 1986)

In this paper were described the most important features of the wood of 10 species belonging to different families of the Cuban flora.

Los principales caracteres cuantitativos y cualitativos de cada una de las maderas investigadas se expresan en la Tabla 1.

FAMILIA: ANNONACEAE

Oxandra lanceolata (Sw.) Baill.

(*Uvaria lanceolata* Sw.; *Oxandra virgata* A. Rich.; *Bocogea virgata* Benth. & Hook.)
Nombres vulgares: Yaya, Yaya hembra

Descripción microscópica: Zonas de crecimiento distinguibles, madera poroso-difusa, poros numerosos, 36 poros/mm², en multiples radiales de 2–5 elementos, frecuentemente se observan también solitarios y en conglomerados (Fig. 1). Diámetro tangencial de los solitar os muy pequeños, 35–47–62 μm; pared celular de 4 μm de grosor, con punteaduras intervasculares alternas y redondas. Platinas de perforación simples.

Los elementos de los vasos son de tallas medianas, alcanzando valores de 280–372–456 μm de largo.

El parénquima axial es de tipo apotraqueal, en líneas tangenciales, las que esporadicamente hacen contacto con los vasos. Las series de parénquima están formadas por 2–4 células, las cuales poseen diámetro medio de 13 μm en sección transversal.

Los radios medulares son numerosos, 8/mm, cercanamente homogéneos, aunque esporadicamente se observan células cuadradas formando una fila extrema, las que son tan o ligeramente mas altas que las procumbentes. Los radios son uniseriados y multiseriados de 2–4 células y ancho promedio de 32 μm (Fig. 2 y 3).

Las fibras son de tipo fibrotraqueida con formas poligonales, las que se distribuyen irregularmente. En sección transversal tienen diámetro promedio de 11 μm y pared de 3 μm de grosor. Las fibras son cortas, con valores de 712–1024–1488 μm de largo.

Table 1

Valores medios de los elementos y principales caracteres de las especies estudiadas

Especides	Elementos de los vasos					Parénquima axial		Radios medulares				Fibras		
	Frecuencia/mm^2	Diám tang. en µm.	Pared en µm.	Platinas de perforación	Largo en µm.	Diám. medio en µm.	# de células	Homogéneos	Heterogéneos	Excl. uniseriados	Uni y multiseriados	Diám. medio en µm.	Pared en µm.	Largo en µm.
1. *Oxandra lanceolata*	36	47	4	S	372	13	2–4	+			+	11	3	1024
2. *Spathodea campanulata*	3–4	116	4	S	222	25	2–3		+		+	21	3	865
3. *Tabebuia calcicola*	20	64	2.3	S	270	22	2–6	+			+	12	2	801
4. *Laguncularia racemosa*	16	79	7	S	429	21	2–8	+		+		13	4.5	883
5. *Grimmeodendron eglandulosum*	14	80	4.5	S	534	15	4–9	+		+		14	5	913
6. *Leucocroton Moncadae*	36	49	5	S	500	13	3–8		+	+		13	3	642
7. *Pseudolmedia spuria*	11	103		S	406	18	2–5		+		+	17	5	1166
8. *Rhizophora mangle*	23	70	5	E	820		2–8	+			+	26	9.5	1635
9. *Symplocos strigillosa*	40	62	2.5	E	1302	22	2–12		+		+	23	4	2221
10. *Celtis tqineqvia*	18	45	8	S	575	17	2–4		+		+	17	5	1032

Leyenda de la Tabla: S = simple; E = escaleriforme

FAMILIA: BIGNONIACEAE

Spathodea campanulata Beauv.

Nombres vulgares: Espatodea

Descripción microscópica: Zonas de crecimiento distinguibles, porosidad difusa, poros escasos, 3–4/mm^2, solitarios, en grupos radiales de 2–3 células y en ocasiones con cierta orien-

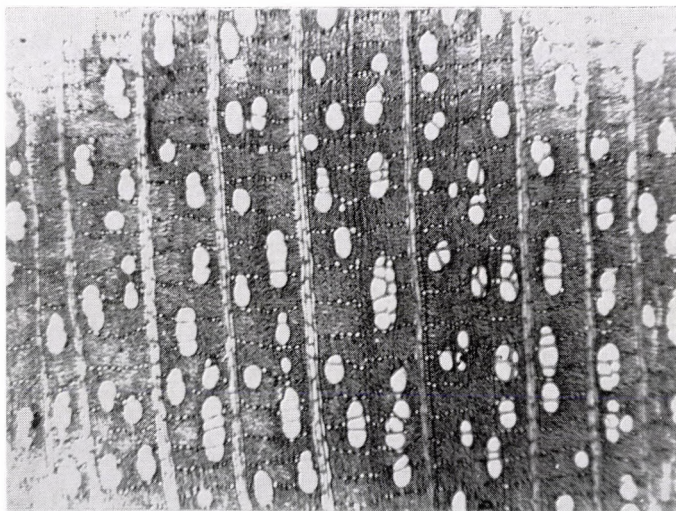



Fig. 1. Oxandra lanceolata (Sw.) Baill. sección transversal, 120×

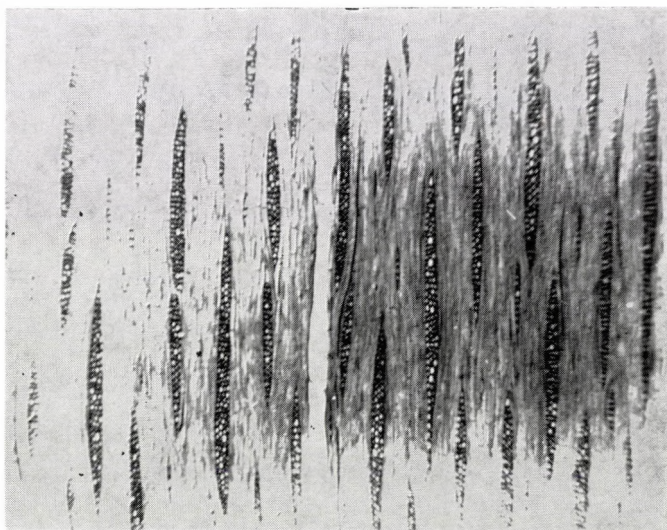



Fig. 2. Oxandra lanceolata (Sw.) Baill. sección tangencial, 120×

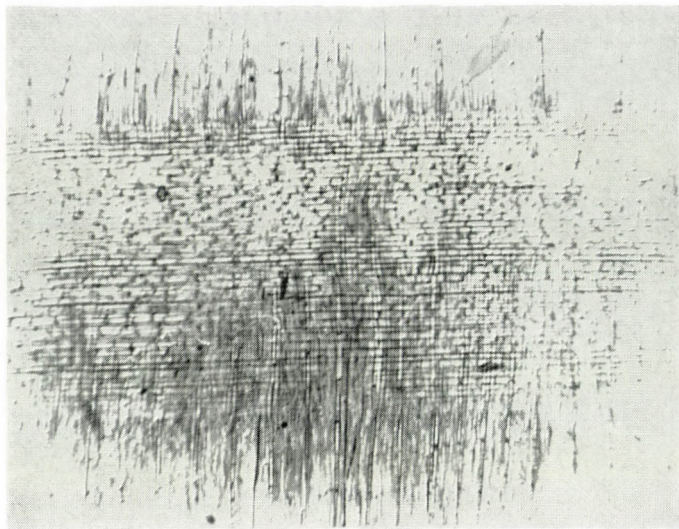



Fig. 3. Oxandra lanceolata (Sw.) Baill. sección radial, 120×

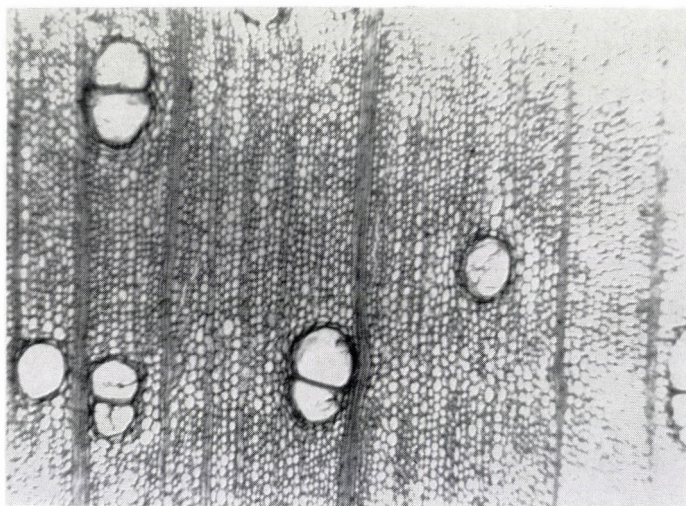



Fig. 4. Spathodea campanulata Beauv. sección transversal, 120×

tación tangencial (Fig. 4). Diámetro tangencial promedio de los solitarios de tallas medianas, 70–116–175 μm. Pared del vaso de 4 μm de grosor.

Elementos vasculares muy cortos con 142–222–323 μm de largo. Punteaduras intervasculares alternas con bordes poligonales y poros lineales. Platinas de perforación simples.

Parénquima axial paratraqueal vasicéntrico y en bandas. Las series del parénquima están constituídas por 2–3 células. En sección transversal las células parenquimáticas tienen 25 μm de diámetro.

Radios medulares uniseriados y multiseriados, heterogéneos, los multiseriados con 2–5 células ó 42 μm de ancho promedio. Moderadamente numerosos, 4–5/mm (Fig. 5 y 6).

Las fibras están distribuídas irregularmente; con formas poligonales. Diámetro medio de 21 μm y pared de 3 μm de grosor Las fibras son muy cortas, con longitudes de 650–865–1075 μm.

Tabebuia calcicola Britt.

Nombres vulgares: Roble caimán.

Descripción microscópica: Anillos de crecimiento inconspicuos, madera con porosidad difusa, poros moderadamente numerosos, 20/mm²; solitarios y ocasionalmente en multiples

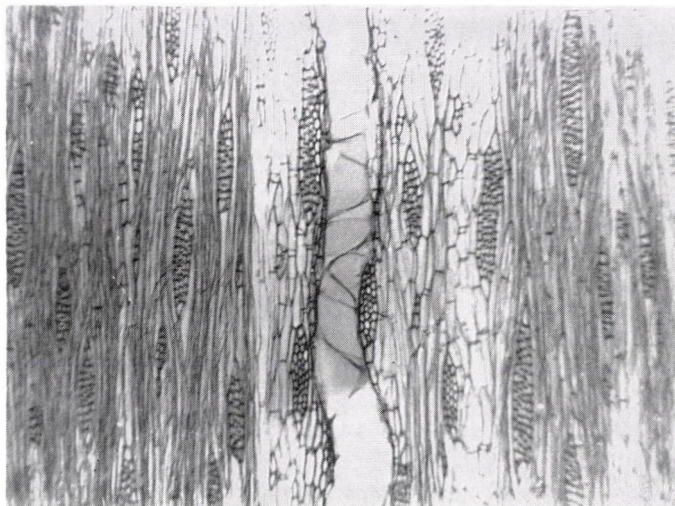



Fig. 5. Spathodea campanulata Beauv. sección tangencial, 120×

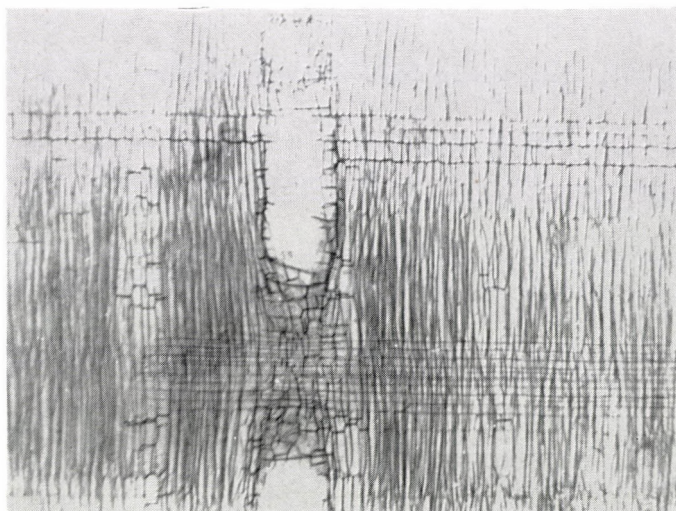



Fig. 6. Spathodea campanulata Beauv. sección radial, 120×

radiales de 2–3 elementos (Fig 7). Diámetro tangencial promedio de los poros solitarios pequeño, 37–64–80 μm; pared celular de 2,3 μm de grosor, con punteaduras areoladas alternas, redondas a ovales y poro a modo de fisura. Platinas de perforación simples.

Los elementos de los vasos son moderadamente cortos, con longitudes de 216–270–328 μm.

Parénquima axial paratraqueal aliforme confluente y en bandas; estratificado. Las series del parénquima están constituídas por 2–6 células, las que en sección transversal poseen diámetro medio de 22 μm.

Los radios medulares son numerosos, 8/mm, homogéneos, formados por células procumbentes; uniseriados y biseriados, estos últimos con ancho promedio de 19 μm. Se observa

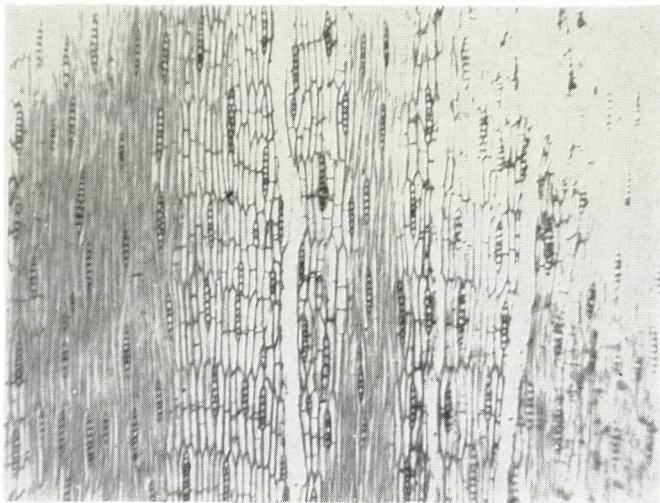



Fig. 7. Tabebuia calcicola Britt. sección transversal, 120×

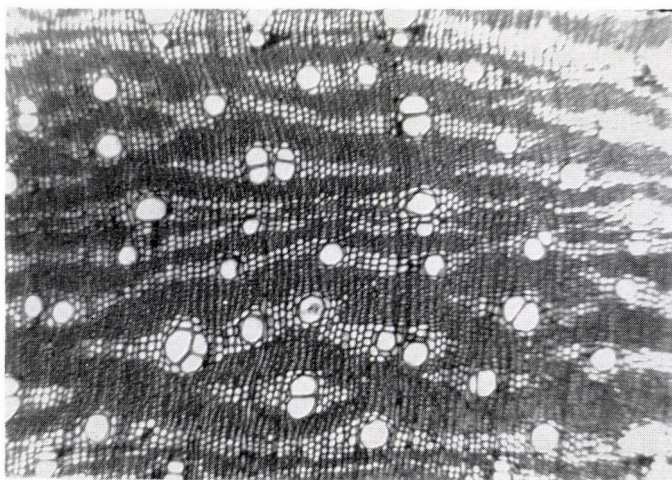



Fig. 8. Tabebuia calcicola Britt. sección tangencial, 120×

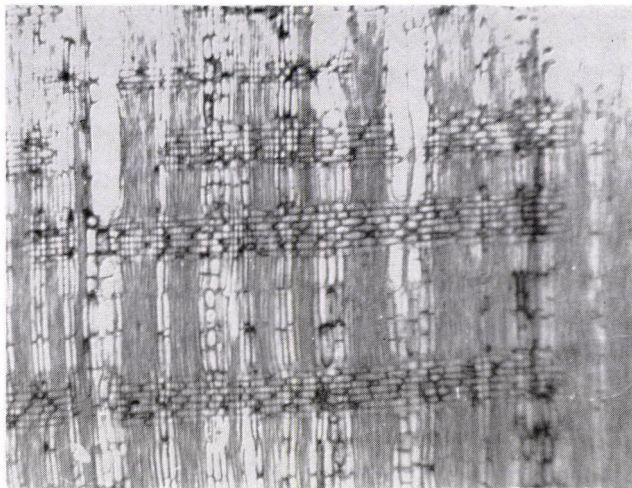



Fig. 9. Tabebuia calcicola Britt. sección radial, 120×

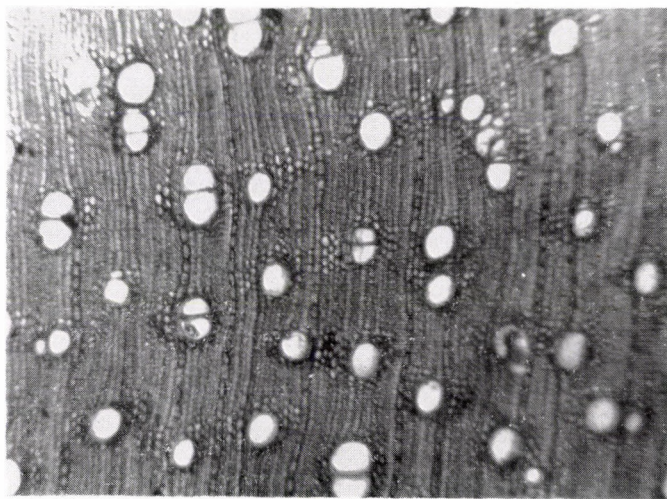



Fig. 10. Laguncularia racemosa (L.) Gaertn. f. sección transversal, 120×

frecuentemente contenidos de color carmelita oscuro en el interior de las células (Fig. 8 y 9).

Las fibrotraqueidas son de formas poligonales y se encuentran distribuídas irregularmente. En sección transversal alcanzan diámetro medio de 12 μm y tienen paredes de 2 μm de grosor. La longitud promedia de las fibras es muy corta, con valores de 600–801–1048 μm.

FAMILIA: COMBRETACEAE

Laguncularia racemosa (L.) Gaertn. f.

(*Conocarpus racemosa* L.)
Nombres vulgares: Patabán

Descripción microscópica: Porosidad difusa, poros moderadamente numerosos, 16/mm^2. solitarios, en multiples radiales de hasta 4 células, raramente en grupos tangenciales de 2–3 y eventualmente en conglomerados de pocas células (Fig. 10). Diámetro tangencial promedio de los solitarios pequeño, 50–79–100 μm. Pared celular de 7 μm de grosor, con punteaduras alternas con bordes circulares y poros lineales, ornadas. Platinas de perforación simples. Los elementos vasculares son cortos, con dimensiones de longitud de 304–429–522 μm. El parénquima axial es paratraqueal aliforme a aliforme confluente. Diámetro celular en sección transversal de 21 μm. Las series del parénquima están constituídas por 2–4–8 células.

Los radios medulares son numerosos, 10/mm, uniseriados y homogéneos, con presencia de cristales y un ancho promedio de 17 μm (Fig. 11 y 12).

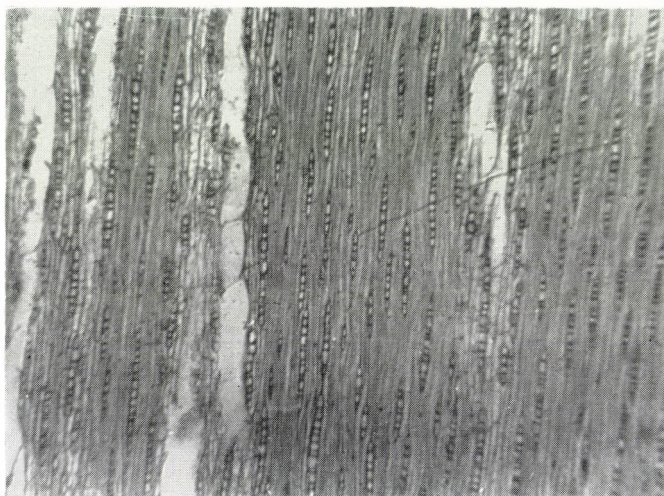



Fig. 11. Laguncularia racemosa (L.) Gaertn. f. sección tangencial, 120×

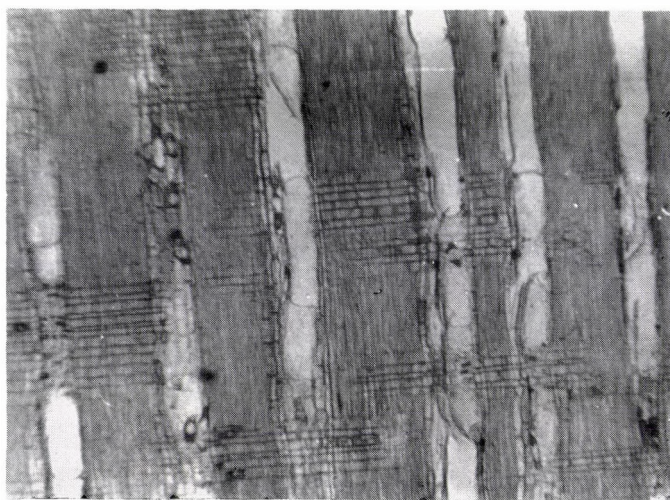



Fig. 12. Laguncularia racemosa (L.) Gaertn. f. sección radial, 120×

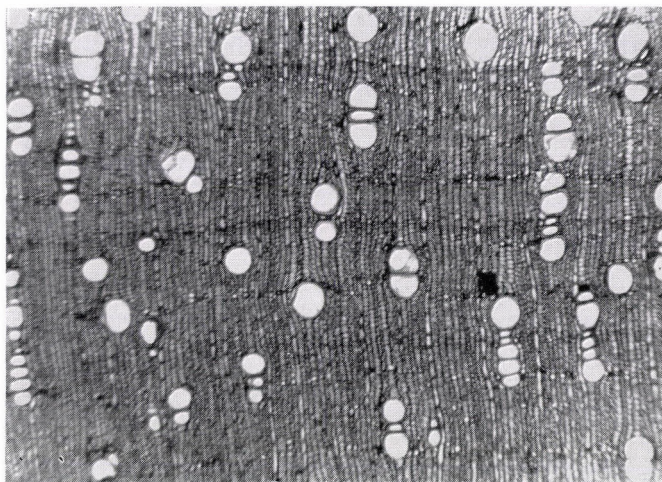



Fig. 13. Grimmeodendron eglandulosum (A. Rich.) Urb. sección transversal, 120×

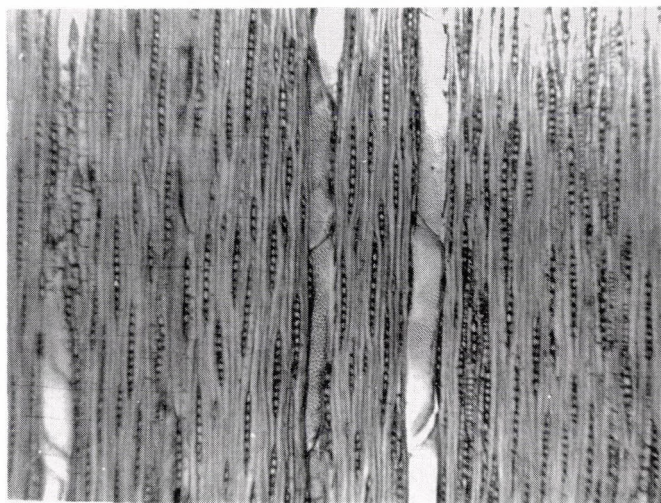



Fig. 14. Grimmeodendron eglandulosum (A. Rich.) Urb. sección tangencial, 120×

Las fibras presentan formas poligonales con tendencia a la orientación radial. Diámetro celular medio de 13 μm y paredes celulares de 4,5 μm. Las fibras son cortas, alcanzando longitudes de 575–883–1300 μm.

FAMILIA: EUPHORBIACEAE

Grimmeodendron eglandulosum (A. Rich.) Urb.

(*Stillingia eglandulosa* A. Rich.; *Excoecaria Sagrei* Muell. Arg.; *E. eglandulosa* Muell. Arg.)

Nombres vulgares: Manzanillo, Manzanillo de monte, Piñipiñi.

Descripción microscópica: Madera que presenta bien marcado el duramen de color rojizo y la albura crema. Zonas de crecimiento no definidas, madera poroso-difusa, poros moderadamente numerosos, 14/mm^2, solitarios, en multiples radiales de varios elementos, muy frecuentes en grupos complejos (Fig. 13). Diámetro tangencial promedio de los solitarios pequeño, 51–80–109 μm, grosor de la pared 4,5 μm, con punteaduras intervasculares alternas y poligonales. Platinas de perforación simples.

Los elementos de los vasos son de tallas medianas, con dimensiones de 272–534–800 μm de largo.

El parénquima axial presenta dos patrones de distribución: apotraqueal en líneas cortas tangenciales de hasta 6 células y paratraqueal escaso, mayormente unilateral. Las

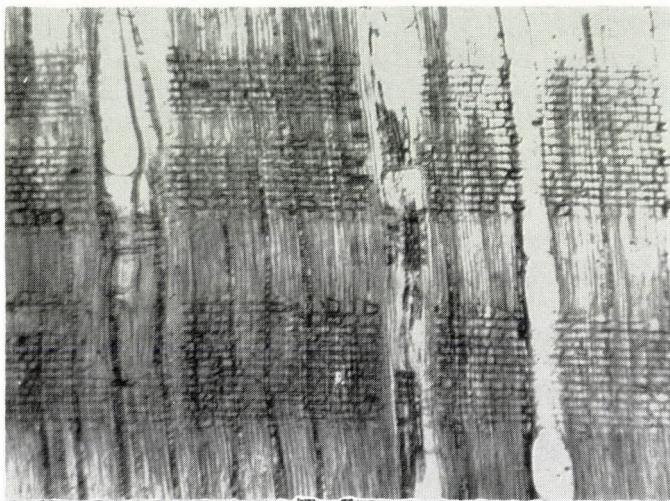



Fig. 15. Grimmeodendron eglandulosum (A. Rich.) Urb. sección radial, 120×

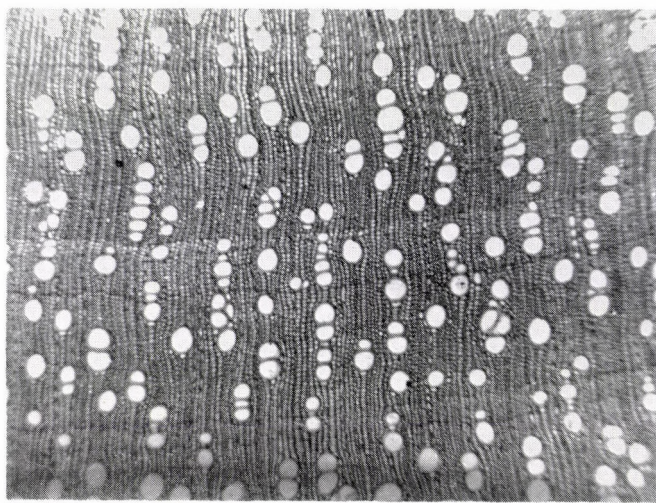



Fig. 16. Leucocroton Moncadae Borhidi, sección transversal, 120×

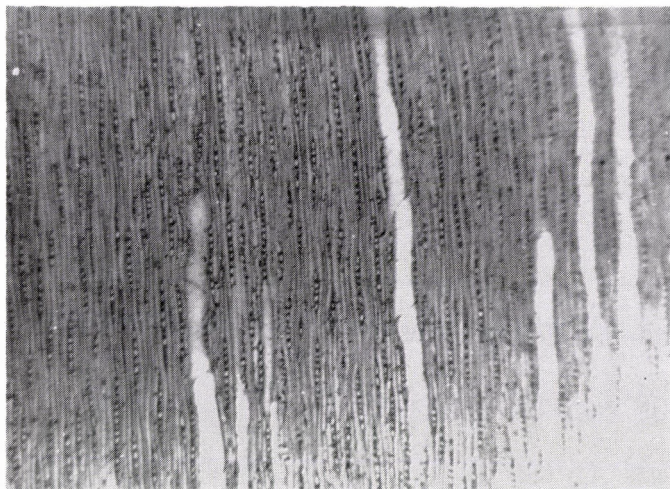



Fig. 17. Leucocroton Moncadae Borhidi, sección tangencial, 120×

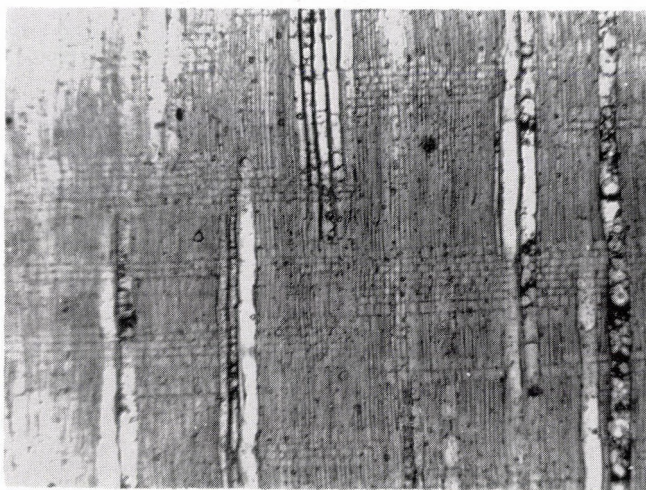



Fig. 18. Leucocroton Moncadae Borhidi, sección radial 120×

células del parénquima presentan contenidos de color carmelita oscuro. Las series están constituídas por 4–9 células, las que en sección transversal poseen diámetro medio de 15 μm. Se observan además células cristalíferas septadas con cristales poliédricos.

Los radios medulares son numerosos, 10/mm, homogéneos y exclusivamente uniseriados, con ancho promedio de 14 μm. Estos radios están constituídos por células procumbentes con contenidos carmelita oscuro (Fig. 15 y 16).

Las fibrotraqueidas tienen formas cuadradas a poligonales y están distribuídas radialmente. En sección transversal tienen diámetro promedio de 14 μm y pared de 5 μm de grosor. Las fibras son muy cortas, con valores de 624–913–1280 μm de largo.

Leucocroton Moncadae Borhidi

Nombres vulgares:

Descripción microscópica: Anillos de crecimiento bien distinguibles, madera con porosidad difusa, poros numerosos, 36/mm^2, mayormente en multiples radiales de 2–8 elementos, ocasionalmente hasta 20, solitarios y en grupos complejos (Fig. 16). Diámetro tangencial promedio de los solitarios muy pequeño, 30–39–65 μm; pared celular de 5 μm de grosor con punteaduras areoladas redondas a poligonales y alternas. Platinas de perforación simples. Los elementos de los vasos son de tallas medianas, con longitudes de 390–500–600 μm.

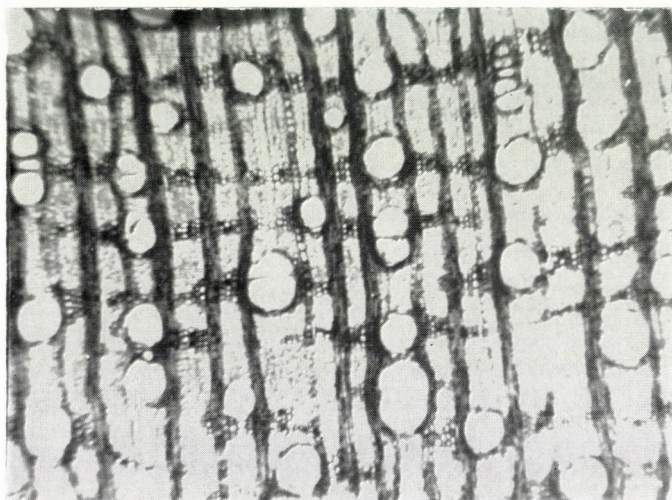



Fig. 19. Pseudolmedia spuria (Sw.) Griseb. sección transversal, 120×

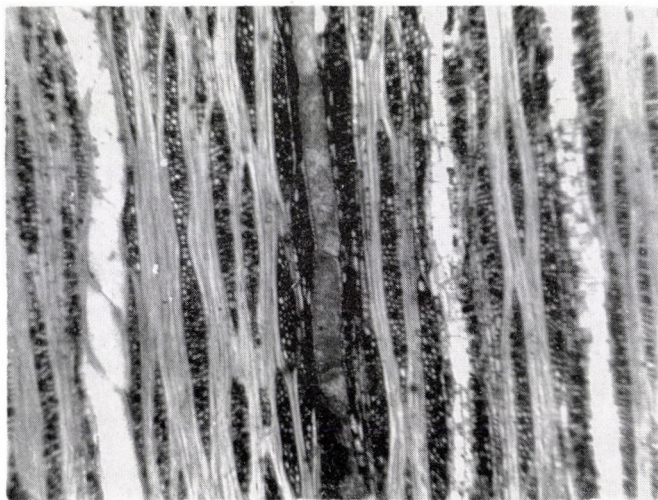



Fig. 20. Pseudolmedia spuria (Sw.) Griseb. sección tangencial, 120×

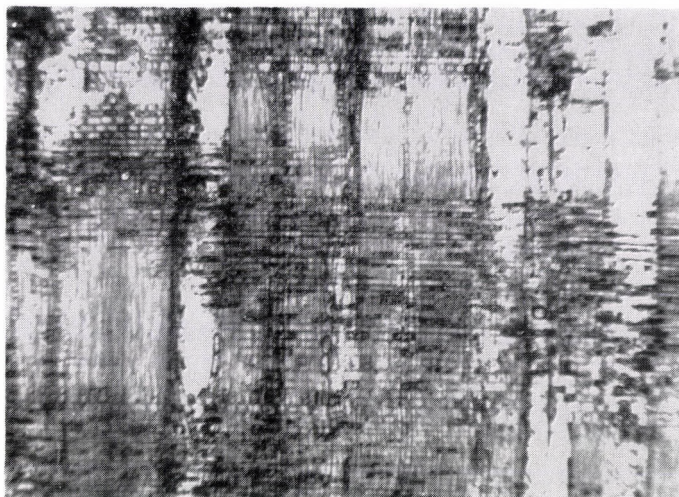



Fig. 21. Pseudolmedia spuria (Sw.) Griseb. sección radial, 120×

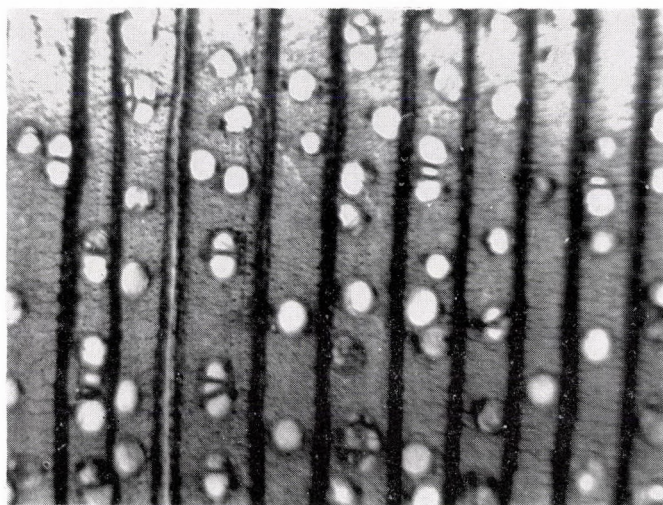



Fig. 22. Rhizophora mangle L. sección transversal, 120×

El parénquima axial es mayormente paratraqueal escaso, aunque ocasionalmente se observan células apotraqueales dispersas (difuso). Las series están constituídas por 3–8 células. las cuales poseen diámetro medio de 13 μm en sección transversal.

Los radios medulares son muy numerosos, 15/mm, heterogéneos y casi exclusivamente uniseriados, raras veces de dos células de ancho. Ancho promedio de 13 μm (Fig. 17 y 18).

Las fibras son de tipo fibrotraqueidas, con formas poligonales y distribuídas radialmente. En sección transversal alcanzan un diámetro medio de 13 μm y pared de 3 μm de grosor. La longitud promedio de estos elementos es muy corta, con valores de 392–642–968 μm de largo.

FAMILIA: MORACEAE

Pseudolmedia spuria (Sw.) Griseb.

(*Brosimum spurium* Sw.)

Nombres vulgares: Macagua

Descripción microscópica: Porosidad difusa, poros moderadamente numerosos, 11/mm², solitarios y en multiples radiales de 2–6 elementos (Fig. 19). Diámetro tangencial promedio

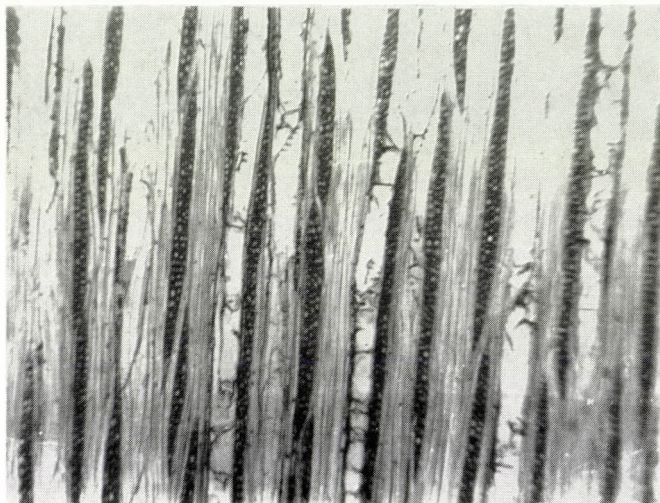



Fig. 23. Rhizophora mangle L. sección tangencial, 120×

Fig. 24. Rhizophora mangle L. sección radial, 120×

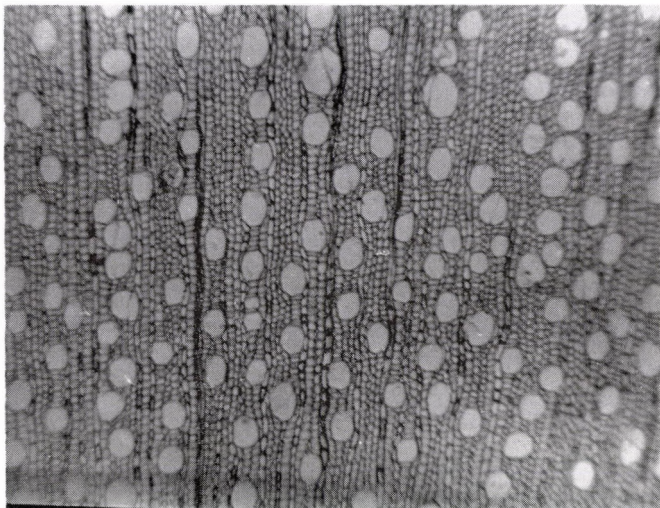



Fig. 25. Symplocos strigillosa Krug et Urb. sección transversal, 120×

moderadamente pequeño, 85–103–135 μm. Las paredes presentan punteaduras intervasculares con bordes redondos y poros lineales. Platinas de perforación simples.

Los elementos vasculares son cortos, alcanzando dimensiones de 285–406–702 μm de largo.

Parénquima axial paratraqueal en bandas confluentes de 3–4 células de ancho con contenidos rojizos. Las series están formadas por 2–4–5 células, las que en sección transversal tienen diámetro promedio de 18 μm. Se observan células cristalíferas septadas con cristales poliédricos.

Los radios medulares son numerosos, 9/mm, heterogéneos, uniseriados y multiseriados de 3–4 células de ancho ó 46 μm de ancho promedio (Fig. 20 y 21).

Las fibras presentan formas poligonales a ovales y se encuentran distribuídas irregularmente. Diámetro medio en sección transversal 17 μm y pared de 4,5 μm de grosor. Estos elementos son cortos, con longitudes de 850–1166–1425 μm.

FAMILIA: RHIZOPHORACEAE

Rhizophora mangle L.

Nombres vulgares: Mangle colorado, Mangle rojo

Descripción microscópica: Madera con porosidad difusa, poros numerosos, 23/mm^2, solitarios, en grupos radiales de 2–6 y conglomerados de 3–4 células (Fig. 22). Diámetro tangencial promedio moderadamente pequeño, 49–70–88 μm, pared de 5 μm de grosor con punteaduras escaleriformes. Platinas de perforación escaleriformes. Se observa la presencia de sustancias carmelitas y tílides en el interior de estos elementos.

Los elementos del los vasos son moderadamente largos, con dimensiones de 517–820–1176 μm de largo.

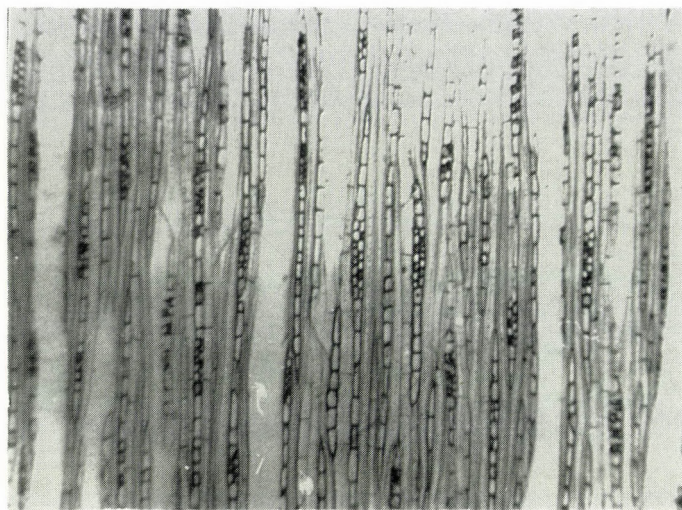



Fig. 26. Symplocos strigillosa Krug et Urb. sección tangencial, 120×

El parénquima axial es paratraqueal difuso. Las series están constituídas por 2–8 células, mas frecuentemente 6.

Los radios medulares son numerosos, 7/mm, homogéneos, uniseriados y multiseriados de 2–4 células de ancho ó 36 μm de ancho promedio. Se observan muy abundantemente cristales poliédricos, así como contenidos de color carmelita en el interior de las células (Fig. 23 y 24).

Las fibras tienen formas poligonales y están distribuídas irregularmente. En sección transversal tienen diámetro medio de 26 μm y pared de 9,5 μm de grosor. Las fibras son como promedio largas, con longitudes de 1000–1635–2750 μm.

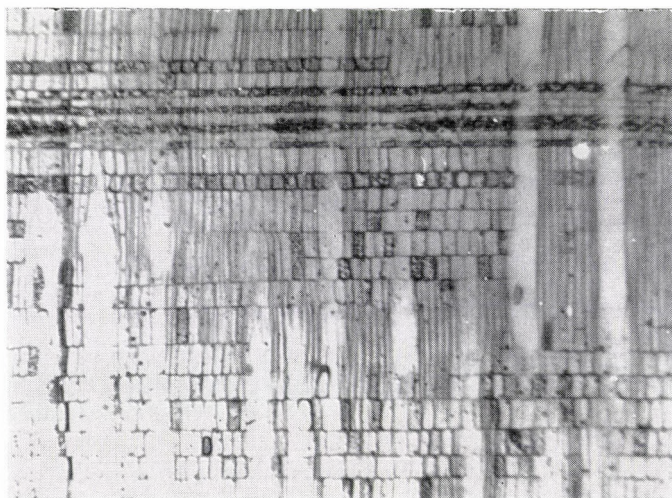



Fig. 27. Symplocos strigillosa Krug et Urb. sección radial, 120×

FAMILIA: SYMPLOCACEAE

Symplocos strigillosa Krug & Urb.

(*S. martinicensis* Griseb. no Jacq.)

Nombres vulgares: Azulejo de pinar, Jibacoa.

Descripción microscópica: Zonas de crecimiento no distinguibles, madera porosa-difusa, poros numerosos, 40/mm², ligeramente angulosos y casi exclusivamente solitarios (Fig. 25). Diámetro tangencial promedio de los poros solitarios pequeño, 45–62–75 μm; pared de 2,5 μm

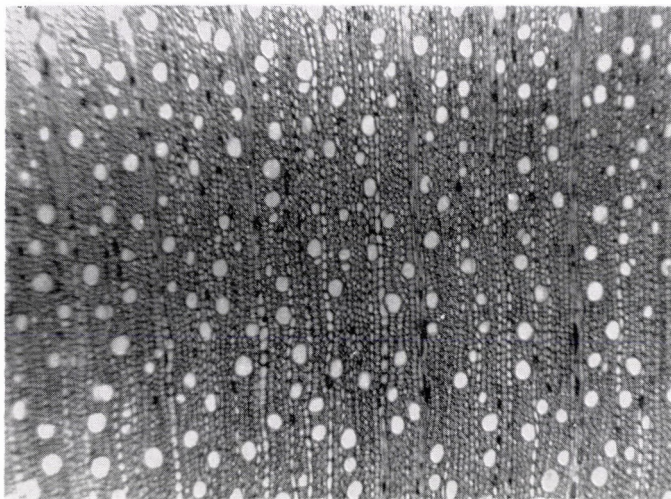



Fig. 28. Celtis trinervia Lam. sección transversal, 120×

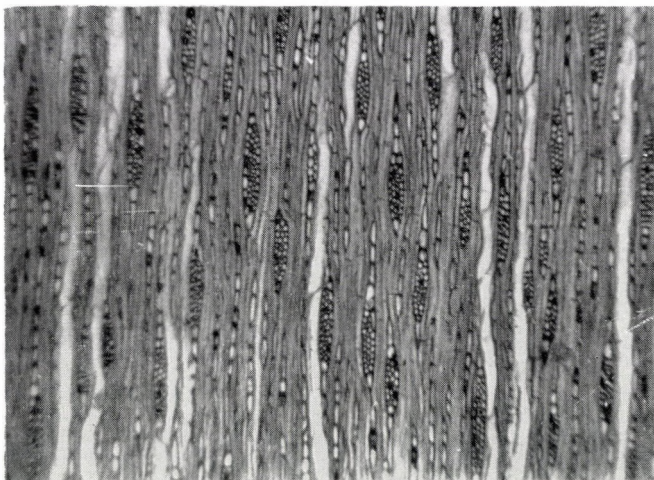



Fig. 29. Celtis trinervia Lam. sección tangencial, 120×

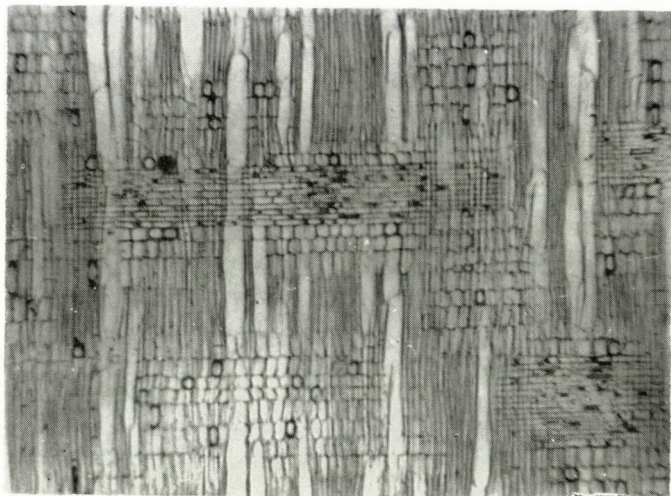



Fig. 30. Celtis trinervia Lam. sección radial. 120×

de grosor con punteaduras intervasculares opuestas, de transición y escaleriformes. Platinas de perforación escaleriformes.

Los elementos de los vasos son muy largos, con longitudes de 456–1302–1738 μm. Parénquima axial mayormente apotraqueal difuso, en ocasiones formando cortas líneas de 3–4 células; esporadicamente se observan células aisladas en contacto con los poros. Las series están constituídas por 2–12 células, con diámetro medio de 22 μm en sección transversal.

Los radios medulares son muy numerosos, 13/mm, heterogéneos, y de dos tipos: uniseriados y biseriados, raras veces 3 series de ancho. Los multiseriados con ancho promedio de 26 μm (Fig. 26 y 27).

Las fibrotraqueidas son de formas cuadradas a poligonales y presentan distribución radial. El diámetro de éstas en sección transversal es de 23 μm, y la pared de 4 μm de grosor. Las fibras son muy largas y alcanzan dimensiones de 1694-2221–2926 μm de largo.

FAMILIA: ULMACEAE

Celtis trinervia Lam.

(*Sponia trinervia* Decne.)

Nombres vulgares: Aguedita, Ramón de Sierra, Ramón de costa, Guasiriano, Hueso, Guanasa.

Descripción microscópica: Anillos de crecimiento poco distinguibles, madera porosodifusa, poros moderadamente numerosos, $18/mm^2$, solitarios, ligeramente angulosos (Fig. 28). Diámetro tangencial promedio de los solitarios muy pequeño, 26–45–57 μm, grosor de la pared de 8 μm, con punteaduras areoladas, redondas, alternas y diminutas con poros redondos. Platinas de perforación simples y ligeramente inclinadas.

Los elementos de los vasos son como promedio de tallas medianas, con valores de 392–575–880 μm de largo.

El parénquima axial es mayormente apotraqueal difuso, aunque ocasionalmente se observan células de éste en contacto con los vasos. Las series están contituídas por 2–4 células, las que en sección transversal poseen diámetro medio de 17 μm.

Los radios medulares son muy numerosos, 15/mm, heterogéneos y de dos tipos: uniseriados y multiseriados de 3-4 células de ancho. Los multiseriados poseen ancho medio de 32 μm (Fig. 29 y 30). En el interior de las células se observan contenidos oscuros.

Las fibrotraqueidas poseen formas poligonales y su distribución es cercanamente radial. En sección transversal tienen diámetro promedio de 17 μm y pared de 5 μm de grosor. Las fibras son cortas, con dimensiones de 800–1032–1344 μm de largo.

Acta Botanica Hungarica 33 (3—4), pp. 353—370 (1987)

PHYCOPHYSIOLOGICAL RESEARCHES IN TRANSYLVANIA

F. NAGY-TÓTH and A. BARNA

BIOLOGICAL RESEARCH CENTER, CLUJ-NAPOCA, RUMANIA

(Received: 10. March, 1985)

The results of the experiments discussed tend to argue the necessity of the development and maintenance of an algal pure culture collection (which at present comprises about 250 species/strains) and the suitability of selected algae for biotechnologies proposed for the near future. The experiments were performed both in static and intensive (bubbled) batch cultures for which some 30 algal species) strains were successively used. The main purpose of researches was to find the most favourable growth conditions based on waste waters as nutritive substrate for a profitable biomass production.

While pursuing the main and much desired purpose the researches produced other interesting results too, e.g. the bioconversion efficiency of N, which seems to obey MITSCHERLICH's rule; the correlation of absorption spectra of chlorophyll *a* and *b*, and the carotenoids with the ontogenetic stages of cells; the converse correlation between the chlorophyll *a*/*b* ratio and the amount of photosynthesized dry matter.

Introduction

A 50 year research work in the physiology of algae in Transylvania was completed five years ago (alas, the anniversary was not mentioned then). The first study dealt with the importance of pure cultures of algae (GRINTZESCO, 1930). During this half century the Transylvanian algology was shaken twice by losing its experimental base — the collection of pure cultures of algae. The first collection, established by GRINTZESCO and PÉTERFI, perished as a consequence of World War II, while the second, set up by PÉTERFI, was spoiled due to a tendency in researches inauspicious for phycophysiology in the post-war time (Fig. 1). However, this half century of Transylvanian researches and the 25 year work of the Clujian Biological Research Center were concluded by 107 studies published — as a proof of a progress both in the quality and quantity of investigations.

The results of the phycophysiological researches carried out in the Clujian Laboratories have been already surveyed (PÉTERFI, 1967; PÉTERFI et al., 1976), therefore in this paper researches published during the last decade will only be summarized. These —too followed the well found main scope of preceding studies: floristic and ecological morphological and structural, physiological and biochemical investigations of algae occurring in the biotops of this country in order to establish a collection of species and strains well defined and many-sidedly characterized for evidencing their bioproductive and bioaccumulative capacity. Based

This 2nd review (the 1st was published by PÉTERFI et al., 1976) was prepared for the 25th anniversary of the Clujian Biological Research Center and the 50th anniversary of the Transylvanian phycophysiological researches.

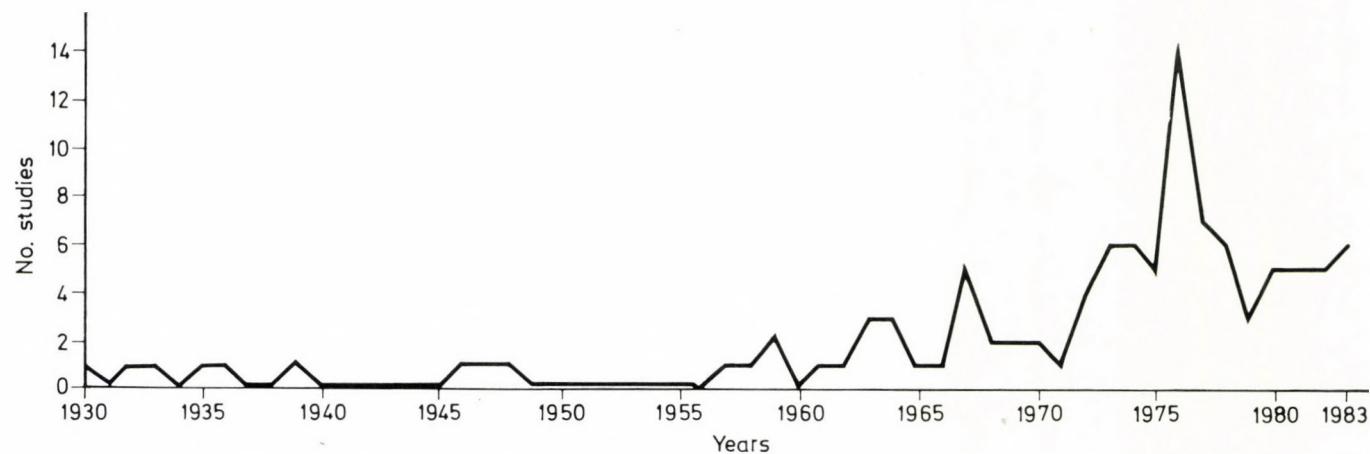



Fig. 1. Studies on phycophysiology published by Transylvanian algologists between 1930–1983

on an adequate number of reliable data the algal bio-fund would serve (in due time) for multiple biotechnologies so much coveted (unconventional source of raw materials, natural fodder, aquaculture, N_2-fixation, etc.).

Materials and methods

Pure cultures of algae are indispensable for any phycophysiological experiments. GRINTZESCO already pointed out in 1930 that pure cultures "constitute the only reliable method for the study of ecology, ontogeny, morphology and physiology . . . which allow to draw trustwothy conclusions from physiological experiments", and in 1978 GEORGE warned that "it is almost impossible to predict where the biological science will advance next and hence dangerous to assume that any particular cultures are useless".

The present-day collection of algal pure cultures (preserved by NAGY-TÓTH, BARNA and DRAGOȘ) of the Clujian Algological Laboratories amounts to 250 species and strains isolated from various habitats of the country, some of which have already vanished (e.g. Porţile de Fier, Porta Ferrea of the Danube). In the phycophysiological researches discussed in this paper, some 30 autochthonous and 2 received (from the Hungarian Natural History Museum, Budapest) species and strains were used.

In respect of phycophysiology, to put in laboratory pure culture algae collected from different habitats, it seems necessary to try many artificial culture media in order to find the most proper and selective one for the isolated species or strains. This attempt seems to be a compulsory measure in each case for every algal sample due to the diversity (structural and functional) of algae (ELLIS, MACHLIS, 1968). That procedure could only ensure the establishing of the best life conditions which satisfy the shortest possible generation time, considered normal from a physiological point of view (LORENZEN, 1974). Conditions in natural habitats are seldom optimal for same species (in case of water/or soil bloom only) LUCAS (cit. PROVASOLI, 1958)). It follows, therefore, that searching for the adequate artificial medium is essential not only for the selection of species/or strains from raw cultures, but at the same time in order to evidence the biological potential of the organisms as well. It was asserted that sophisticated phycophysiological experiments would be performed only with synchronized algae, the results of the other researches being considered not quite conclusie (LORENZEN, SCHLEIF, 1966).

Results

Investigations intending to establish the proper nutritive demands of algae could be considered, in a broad sense, as an assay (test) procedure (WEISS, 1971), as well as a means of bringing the factors in such physiologically harmonious correlations which promotes the synthesis of a certain (expected) substance (directed biosyntheses). In that sense the published studies comprise data of experiments concerning:

1. trying, as well as modifying known artificial media;

2. supplementing known artificial media with physiologically active (growth) substances;

3. finding of new media based on waste (or natural) waters.

1. Researches relating to trying and modifying previously known artificial media aimed, essentially, at finding out the consequences of:

a) changing the composition and concentration of the nutrients;

b) changing the proportion of some macro- and

c) micro-elements, and

d) altering of the pH of the media.

1.a. *Phormidium viscosum* was grown in static cultures (in test tubes of 20 ml containing 10 ml nutrient solution, and in Erlenmeyer flasks of 100 ml containing 50 ml nutrient solution) and in intensive (bubbled with CO_2 enriched sterilized air, 70 ml/min/100 ml algal suspension) batch cultures (in modified (NAGY-TÓTH, 1972) *Vladimirova-Semenenko*'s vessels of 275 ml

containing 200 ± 10 ml solution) in the following artificial nutrient solutions: *Benecke*–K_2HPO_4; *Benecke*–KH_2PO_4; *Witsch; Knop–Pringsheim; Knop–Pringsheim–Felföldy; Allen–Arnon; Sălăgeanu; Watanabe; Moyse; Gorham.* It was found that *Watanabe*'s and *Knop–Pringsheim–Felföldy*'s media, in which the variation of cell dimensions became the most reduced were favourable. It is interesting to mention that the liquid of the cultures and the extract of the cells of these two media were the most inhibitory on the *Lepidium*-test (FABIAN et al., 1981).

1.b. Proportion of the macroelements C, N and P was alternated in order to optimize the growth conditions (static and intensive) of *Spirulina platensis.* Quantities of $NaNO_3$ and K_2HPO_4, or $NaNO_3$ and $(NH_4)_2HPO_4$, or $(NH_4)_2HPO_4$ by itself were put into *Zarrouk*'s solution so that the ratio of N : P was 0.9 : 1; 2.75 : 1; 5.5 : 1 and 11 : 1, meanwhile the concentration of CO_2 in the bubbling air mixture was 1.5 and 5%, respectively. The nutritive solutions were made with bidist. water, dam lake water (near Gilău), or dairy waste water. The amount of biomass photosynthesized and its protein (soluble) content attested that the most proper ratio of N : P was 5.5 : 1 and the optimum CO_2 concentration 1.5% (Fig. 2). In cultures grown in solution mahe with waste water, in which the nutrients were halved, the productivity dropped to 30% (in comparison to *Zarrouk*'s control), though the pigment content of the cells did not differ significantly (NAGY-TÓTH et al., 1982).

1.c. The effect of microelements Zn and Co was studied with *Scenedemus acutiformis.* It was grown intensively in modified *Tamiya* urea-EH solution (i.e. it was supplemented in an amount of 10% with soil extract prepared according to WITSCH (PÉTERFI et al., 1969)). The concentrations of Zn and Co increased 10× (compared to that in *Tamiya*'s solution) hindered the multiplication of cells (measured by cell- and optical-density), as well as the biosynthesis of proteins and carbohydrates, while — surprisingly — their absence improved slightly the growth (Fig. 3) (PÉTERFI et al., 1975). It is appropiate to mention here that Co at concentrations of 0.0016–0.016 mg/l as hexamine-cobalt complex stimulated the multiplication of this alga in static cultures (PÉTERFI, NAGY-TÓTH, 1979).

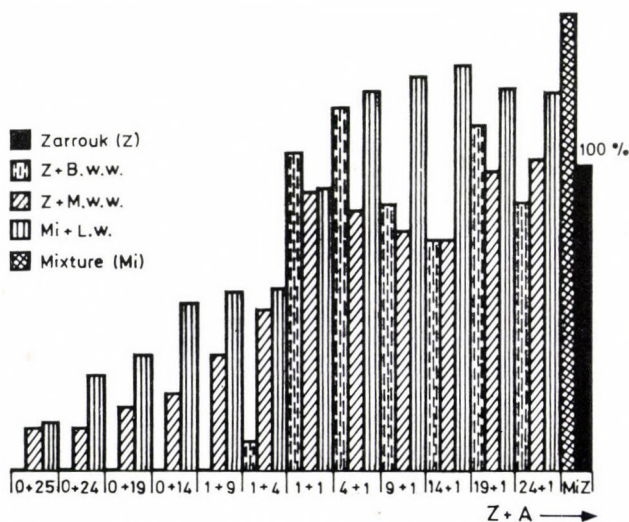



Fig. 2. Growth of *Spirulina platensis* in ZARROUK's solution (Z), and in its mixtures with waste waters (A) of brewery (B), dairy factory (M), with both of them (Mi = 1 Z + (1 B + 1 M)) and in the mixture (Mi) with dam lake water (Mi + Lw) (BARNA et al., 1982)

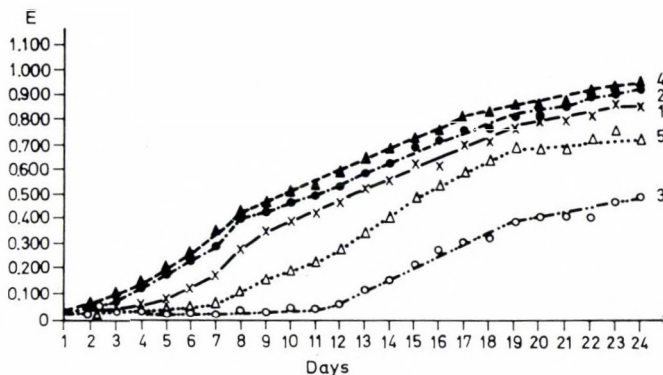



Fig. 3. The effect of cobalt (2, 3) and zinc (4, 5) at normal (2, 4) and in 10 times increased (3, 5) concentrations in modified TAMIYA urea-EH's nutrient solution (1) on the multiplication of intensive cultures of *Scenedesmus acutiformis* (PÉTERFI et al., 1975)

1.d. The effect of pH was checked in two series of experiments carried out with *Scenedesmus acutiformis*, *Stichococcus bacillaris*, *Gloeotila protogenita*, *Microthamnion kützingianum*, *Ulothrix variabilis*, *Stigeoclonium subsecundum* amd *Chaetophora flagellifera* grown simultaneously in modified *Tamiya* urea-EH's, *Bold*'s and *Witsch*'s media. On the basis of multiplication and biomass production it was concluded that for the chlorococcal alga *Scenedemus acutiformis* in intensive culture put in modified *Tamiya* urea EH's medium the pH of 6.5 was more favourable (the production increased by 50%) than that of 5.5. If this medium was diluted to 1 + 1 with "Zizin" mineral water the proper pH became 7.5–8 (the production of biomass increased by 50% compared to pH 5.5, and by 100% to the original *Tamiya*'s medium) (BARNA et al., 1974). The investigated ulothrichacean algae tolerated, in static culture, pH 4, too, but their optimum varied; thus it was 6.6 for *Microthamnion*, 6.7 for *Chaetophora* and *Stigeoclonium*, and 7.7 for *Stichococcus*, *Gloeotila* and *Ulothrix*. The fastest growth was recorded with *Stigeoclonium* while the slowest one with *Stichococcus* (PÉTERFI, MARTON, 1977).

2. Supplementation of the pre-existing media with physiologically active substances was intended to improve the total life conditions of the algae, i.e. the more efficient exploitation of the available nutritional pool. The effects of the procaine were tested in two ranges of concentrations (10–0.00001 and 0.4–0.04 mg procaine/l) dissolved in *Knop–Pringsheim*'s, as well as in *Tamiya* urea-EH's solutions. The test alga was *Stichococcus bacillaris* grown in static (Erlenmeyer flasks of 100 ml containing 50 ml algal suspension) and in intensive (vertical columns of Ø = 2, L = 50 cm, containing 100 ml algal suspension) cultures. The measurements (optical and cell densities) proved that under static conditions (during 21 and 60 days, respectively) concentration of 0.1, 0.25 and 0.075 mg procaine/l, while under intensive conditions (during 15 days) 0.20 mg procaine/l stimulated the multiplication of the alga (MARTON et al., 1974a, 1974b). Other experiments also demonstrated that procaine in a concentration of 0.10 mg/l put in *Knop–Pringsheim*'s, *Tamiya* nitrate-A's, *Tamiya* urea-EH's and modified *Tamiya* urea-EH's solutions had antiseptical, bacteriostatic, fungistatic effects on *Stichococcus* cultures (MARTON, 1975).

Some antibiotic, antiseptical and fungicidal substances (penicillin, streptomycin, erythromycin, tetracyclin, solvocillin, chloramphenicol, efitard, nistation, fenosept, Na-benzoat, captan, dithan-M) were also tested on *Stichococcus bacillaris* grown under static conditions (in test tubes, Erlenmeyer flasks). These substances were put in *Knop–Pringsheim*'s solution at concentrations of 0.4, 1, 4, 10, 40, 50, 100, 200, 300, 400 and 1000 mg/l. Data

(optical and cell densities) recorded (after 45 days) demonstrated the selective action on the alga, and its accompanying microflora; stimulating or inhibiting their multiplication, depending on doses and structures of the substances. Peculiar morphoses were not recorded (MARTON, 1973a, b).

The tolerance of *Stichococcus bacillaris* was experimented (with static cultures, in Erlenmeyer flasks of 100 ml containing 40 ml *Knop–Pringsheim*'s solution) for some chloromethyle-oxazole derivatives, too. These substances generally had an adverse effect on the multiplication (optical and cell densities) and pigment content of cells (after a cultivation of 1, or 9 weeks). The effect depended on the position of radicals to the phenolic) ring (MARTON, CHINDRIȘ, 1974; TĂMAȘ et al., 1975). Other experiments showed, however, that phenol as well as detergents (Trial, Dero Crystal dissolved in *Zehnder–Gorham*'s solution) enhanced (in continuously illuminated, thermostated static cultures) the growth (optical and cell densities) of *Monoraphidium contortum* (BERCEA et al., 1984).

The very diversified assiduous cultivation of microorganisms and algae revealed — among others — that satisfying multiplication might be determined not only by the harmonious proportion of nutrients, but also by some substances appearing in cultures depending on their initial cell densities (Fig. 4) (PRINGSHEIM, 1954; SKULBEBG, 1966; BUNT, 1968). These substances were conceived as s c h i z o k i n e n e s (hormones which act on the splitting, or division of cells) (LANKFORD et al., 1969) or "superchelators" (HUTNER, 1972). In order to catch some actions of such substances two subsequent experiments were performed with intensive cultures (in vertical columns of Ø = 5, L = 120 cm, containing 1,600 ml of algal suspension, and in parallelepiped plexiglass vessels of $2 \times 14 \times 16$ cm containing 250 ml algal suspension) grown in *Knop–Pringsheim–Felföldy*'s, as well as in modified *Tamiya* urea-EH's solution. Initial cell densities in the cultures varied between 40 and 25,000 cells/μl. The data (optical and cell densities) recorded (at the start of the stationary phase, after 19 and 7 days, respectively) proved that with a lower initial cell density the culture did not reach during the same growth period such a high final cell density as with higher initial cells densities, probably because of the lengthened lag phases (Figs 5, 6). Such a weakening of the algal culture has been considered "p h y s i o l o g i c a l e x h a u s t i o n" (NAGY-TÓTH, 1972). Cultures initiated with higher cell densities had a shorter lag phase, a longer stationary phase and a very highffinal cell density (NAGY-TÓTH et al., 1974).

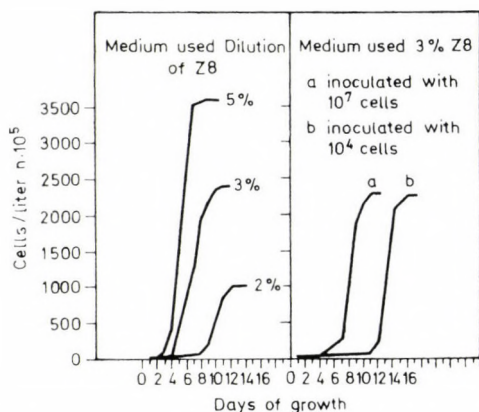



Fig. 4. Multiplication intensity of *Selenastrum capricornutum* determined by the dilution of medium and by the initial cell density (SKULBERG, 1966)

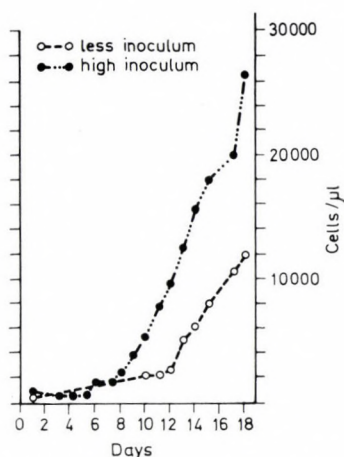



Fig. 5. Dependence of cell multiplication of *Scenedesmus acutiformis* on the initial cell density (NAGY-TÓTH et al., 1974)

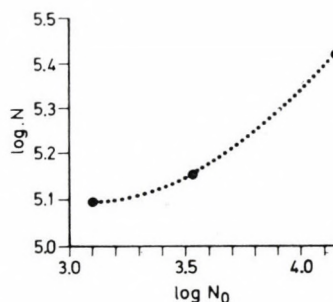



Fig. 6. Relation between initial (No = 1,282; 3,381; 14,112 cells/μl) and final (N = 126,375; 144,050; 269,375 cells/μl) cell densities (end of log-phase of the cultures) of *Scenedesmus acutiformis* in intensive cultures in modified TAMIYA urea-EH's solution (NAGY-TÓTH et al. 1974)

Researches of algal nutrition have made a great progress by the utilization of chelates in preparing nutrient solutions. Though the natural and artificial chelates vary much in composition and structure, in algal nutrition researches EDTA is more frequently utilized. Compared to EDTA (well-known from our own experiments, too). The usefulness of NaFeEDDHA (Sequestrène 138-Fe) was investigated in intensive cultures (installed in parallelepiped plexiglass vessels, modified *Tamiya* urea-EH's solution, waste water from brewery supplemented with KNO_3) of *Scenedemus acutiformis*. Although significant differences (concerning optical and cell densities) did not arise owing to the two chelates, the amounts of biomass produced were nevertheless slightly higher in cultures grown in media with NaFeEDDHA (BARNA, NAGY-TÓTH, 1978).

3. Researches of algal nutrition suggested the utilization of waste waters in preparing nutrient solutions to be adequate for static and intensive cultures, as well as, later on, for massive cultures. It is the Clujian laboratory in Roumania that initiated (in 1968) this project.

The studies (more than 30) carried out in this field of research have proved (like the results of other experts) the doubtless double advantage of the culture of algae based on waste waters: biomass production and water purification.

Many variants of nutrient liquids were made by mixing (in various proportions) different waste waters, or by diluting them with fresh water, or mineral waters, as well as amending them with a few essential nutrient elements (N, P, K). From the combinations experimented the best results were obtained with mixtures based on waste waters of brewery and sugar factory. However, the recorded results differed, of course, depending on the algae cultivated, the level of perfection and on the size of the experimental device (static cultures in test tubes or Erlenmeyer flasks, intensive cultures in Erlenmeyer flasks or parallelepiped plexiglass vessels, *Vladimirova–Semenenko*'s vessels, and vertical columns as well).

Waste waters of brewery were tested first in various dilutions with drinking water or artificial nutrient solutions in static cultures. After that the most promising variants were checked in intensive cultures, too. One of the earlier experiments (both in static and in intensive cultures) proved that this waste water added in 10% to *Tamiya* urea-EH's solution had a similar beneficial effect on *Scenedesmus acutiformis* as the well-known soil extract. Thus, it was possible to substitute an excellent, but rather variable ingredient of algal nutrient solutions (BARNA, 1978). The test alga *Scenedesmus acutiformis* grew also well in undiluted waste water of brewery enriched with *Tamiya* urea-EH's solution salts, but it multiplied much more if this nutrient liquid was halved with "Zizin" mineral water; thus the amount of the nutrient salts was halved, too. The highest rate of multiplication and consequently the best production (219% dry matter comparing to the *Tamiya* urea-EH's control) were recorded in parallelepiped vessels (due probably to the more favourable illumination, during 12 days of cultivation), while in vertical columns the yield was a little less (173%, after 15 days of cultivation). The total protein content of cells grown in mixtures of 1 + 1 *Tamiya* urea-EH in brewery waste water + "Zizin" mineral water reached 60% (PÉTERFI et al., 1975). The waste water of brewery gained also considerable nutritive values when supplemented with only some indispensable salts (KNO_3, $(NH_4)_2HPO_4$, $CO(NH_2)_2$).fIn mixture of waste water of thermoelectrical plants, sugar factory and brewery (at a ratio of 2 + 1 + 1) supplemented only with KNO_3 (1 g/l), while the multiplication of *Scenedesmus acutiformis* (in intensive cultures grew in gas-washing type vessels during 10 days) was rather slow (hardly 30% in comparison to the modified *Tamiya* urea-EH's solution used as control), the final biomass production (over 50%) and the chlorophyll and carotenoid contents (40—50%) were a little better, arguing for the increased cell sizes. If this mixture was further completed with "Zizin" mineral water (the ratio thus becoming 1 : 1 : 1 : 1) ond $CO(NH_2)_2$ was added (3 g/l), the nutritive value dropped significantly, especially the pigment content was very low. On the other hand, mixtures of waste water from sugar factory and from thermoelectrical plant or geothermal water (at a ratio of 1 : 1) enriched with $(NH_4)_2HPO_4$ (3.3 g/l) solely assured (during 14 days), under intensive conditions (gas-washing type vessels, vertical columns), a multiplication (Fig. 7) and photosynthetic production (dry matter, soluble protein, pigment content) comparable to that in the control — artificial complete nutrient solutions (*Tamiya* urea-EH, *Knop–Pringsheim–Felföldy*) — not only for *Scenedesmus acutiformis*, but all the more for *S. acutus* (PÉTERFI et al., 1977).

The nutritive value of the mixture made from waste waters of sugar factory and thermoelectrical works enriched with *Benecke*'s medium or only with $(NH_4)_2HPO_4$ (3.3 g/l) was also examined using an original device, consisting of inclined troughs (1.1%, i.e. 3 cm in a distance of 258 cm) coated with sponge or pebble, in which fixed filamentous algae or periphyton, i.e. *Ulothrix* sp., *Stigeoclonium* sp. and *Cladophora* sp. were successively grown under streaming (0.136–0.180 l/s) recycled warm nutrient liquid. It was the goal of these experiments to exploit, as well as to recover the residual heat from thermopolluted water by means of growing algae

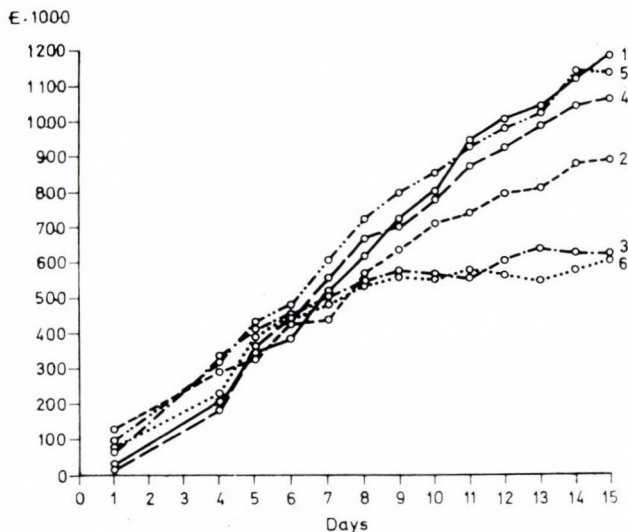



Fig. 7. Growth of *Scenedesmus acutiformis* (1–3) and *Sc. acutus* (4–6) in modified TAMIYA urea-EH's solution (1, 4, control), mixtures of geothermal water and waste water of sugar factory (in proportion of 1 + 1) enriched with $(NH_4)_2HPO_4$ (3.3 g/l) (2, 5) and mixture of waste water of thermoelectric works and sugar factory (in proportion of 1 + 1) enriched with $(NH_4)_2HPO_4$ (3.3 g/l) (3, 6) (PÉTERFI et al., 1977)

of which photosynthetic capacity eventually would be enhanced by higher temperatures (thermophilicity). Noteworthy productivity (5.5 dry matter/m^2/day) was obtained with *Cladophora* sp. growing (for 29 days) in the mixture of the two waste waters enriched only with $(NH_4)_2HPO_4$. However, this result is not an optimal one, it could be compared with those recorded by HINDÁK (1970) by *Koliella spiculiformis* cultivated intensively in glass cuvettes. Along the trough covered with algae the temperature decreased by 1 °C (BARNA, NAGY-TÓTH, 1980).

Nutritive liquids suitable to intensive cultures (in vertical columns) of *Scenedesmus acutus* were prepared from waste waters of brewery and porcelain factory and of Someşul Mic river water (up- and down-stream of Cluj). In this nutritive mixture the rate of multiplication was slow at the beginning (on the first 4 days), but it intensified later on, and at the end of the logarithmic phase (the 11th day) it became practically equal with the control (modified *Tamiya*'s medium) (Fig. 8). The final values of optical and cell densities, as well as that of the photosynthesized biomass were also nearly the same in the experimental variants (or slightly higher in the mixture), whereas the total protein content of the cells was significantly higher. Such a successful growth and bioaccumulation of *Scenedesmus acutus* became completely inhibited if to this very cheap medium waste water of pharmaceutical works was added (PÉTERFI et al., 1978).

Amelioration of waste water of pharmaceutical works for algal nutrition was again attempted by diluting it with waste waters of brewery and porcelain factory, or with drinking water, and enriching the mixtures either with *Benecke*'s, and *Knop–Pringsheim*'s medium salts, or with $(NH_4)_2HPO_4$ by itself. Results recorded for the intensive cultures of *Scenedesmus acutus* (grown in *Vladimi ova–Semenenko*'s vessels) allowed to conclude that the waste water of the porcelain factory subdued markedly the aggressivity of the pharmaceutical works

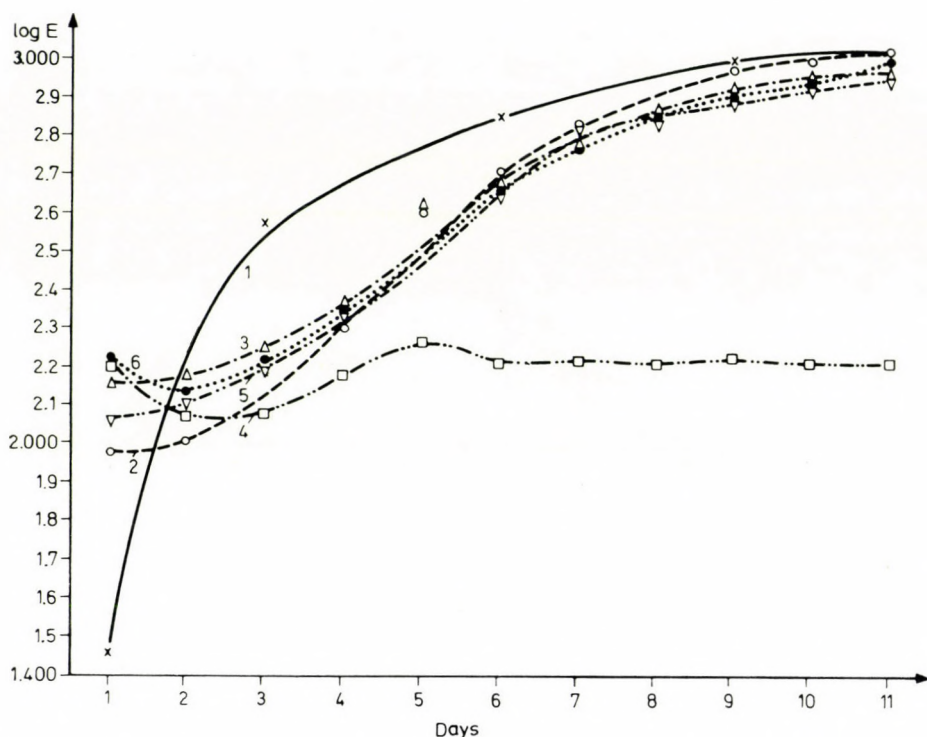



Fig. 8. The growth rate of *Scenedesmus acutus* in intensive cultures in media based on waste waters. 1 — modified TAMIYA urea-EH's solution (control); 2 — mixture of Someş river water (up-stream of Cluj) and waste water of brewery (in proportion of 3 + 1); 3 — mixture of Someş river water (up-stream of Cluj) and waste waters of brewery and porcelain factory (in proportions of 2 + 1 + 1); 4 — mixture of Someş river water (up-stream of Cluj) and waste waters of brewery, porcelain factory and pharmaceutical work (in proportions of 1 + 1 + 1 + +1); 5 — mixture of Someş river water (down-stream of Cluj) and waste water of brewery (in proportions of 3 + 1); 6 — mixture of Someş river water (down-stream of Cluj) and waste waters of brewery and porcelain factory (in proportions 2 + 1 + 1) (PÉTERFI et al., 1978)

water and consequently promoted (in mixtures of 3 + 1 and 1 + 1 enriched with *Benecke*'s medium salts) multiplication, and biomass production, as well as the content in soluble proteins to approximate the level of the cultures grown in solutions without that injurious waste water. The pigment content of the cells, however, was lower and the amount of soluble proteins releaved in the culture liquid higher (NAGY-TÓTH et al., 1976). The waste water of pharmaceutical works could be better improved for *Scenedesmus acutus* and even more for *S. acutiformis*, by mixing it with that of brewery and porcelain factory (at ratios of 1 : 1 and 1 : 1 : 1) where the mixtures were supplemented with either *Knop–Pringsheim*'s medium salts or with $(NH_4)_2HPO_4$ by itself (BARNA et al., 1977).

Some algae were successfully grown (both in static and in intensive cultures) in several mixtures made of waste waters of chicken- and pig-farm, and of dairy factory. Integral, undiluted (but filtered and autoclaved) waste water of chicken-farm assured (in static cultures put in Erlenmeyer flasks) satisfactory multiplication both for *Rivularia* sp. and *Chlorella cf. pyrenoidosa*. Its trophic values dropped considerably by dilution (at ratios between 1 : 0–1 : 49)

either with dam lake water (near Gilău) or with *Benecke*'s nutrient solution. In the integral waste water of pig-farm only *Chlorella cf. pyrenoidosa* could grow. This alga grew also satisfactorily in waste water of dairy factory (diluted either with drinking water or with *Knop–Pringsheim*'s nutrient solution) (Fig. 9). However, the growth of *Scenedesmus acutus* was inhibited in both of these waste waters if undiluted, but dilution or supplementation with a few nutrients even stimulated the process (Fig. 10). The best proportion of dilution for waste water of pig-farm and *Knop–Pringsheim*'s solution or dam lake water proved to be 1 + 7 in which static cultures exceeded slightly the control (Fig. 10), whereas intensive cultures

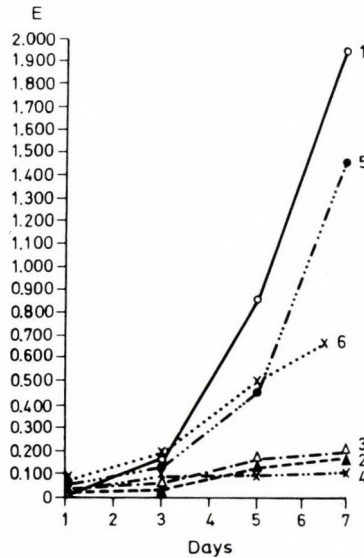



Fig. 9. Growth of intensive cultures of *Chlorella pyrenoidosa* in KNOP-PRINGSHEIM's solution (1) and in mixtures of waste water of dairy factory with KNOP-PRINGSHEIM's solution in proportions of 1 + 2 (2), and 1 + 7 (3), and with dam lake water in proportions of 1 + 7 (4), as well as in mixtures of waste water of pig-farm with KNOP-PRINGSHEIM's solution (5) and with dam lake water (6) in proportions of 1 + 7 (FABIAN et al., 1983)

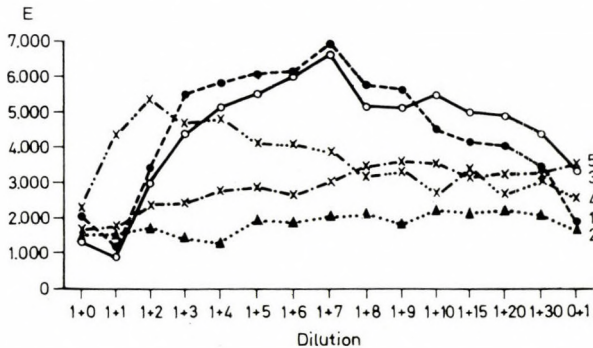



Fig. 10. Multiplication of *Scenedesmus acutus* in static cultures in waste waters of pig-farm (1, 3) and dairy factory (2, 4) diluted with dam lake water (1, 2) or with KNOP-PRINGSHEIM's solution (3, 4) compared to the culture grown in KNOP-PRINGSHEIM—FELFÖLDY's solution (5) (FABIAN et al., 1983)

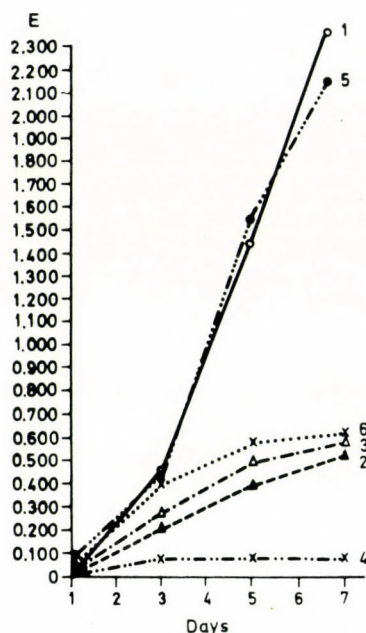



Fig. 11. Growth of intensive cultures of *Scenedesmus acutus* in KNOP-PRINGSHEIM's solution (1) and in mixtures of waste water of dairy factory with KNOP-PRINGSHEIM's solution in proportions of 1 + 2 (2) and 1 + 7 (3), and with dam lake water in proportions 1 + 7 (4), as well as in mixtures of waste water of pig-farm with KNOP-PRINGSHEIM's solution (5) and with dam lake water (6) in proportions of 1 + 7 (FABIAN et al., 1983)

Table 1

The amounts of biomass and its N *and* P *contents of Scenedesmus acutus (initial* E = 0.010; *cells/μl* = 370) *and Chlorella pyrenoidosa (initial* E = 0.010; *cells/μl* = 400) *cultivated (for* 7 *days in batch cultures) intensively in waste water mixtures*

Algae	Mixtures	Cells/μl	Extinction	Dry weight g/l	N° %	P, %	Proteins %
Scenedesmus acutus	CPo + LG = 1 + 7	25.312	0.668	1.40	0.94	1.02	5.90
	CPo + KP = 1 + 7	190.000	2.120	5.54	2.85	0.65	17.80
	ICIL + LG = 1 + 7	5.615	0.120	0.26	3.00	1.19	18.80
	ICIL + KP = 1 + 7	56.562	0.628	1.04	8.63	2.05	54.00
	ICIL + KP = 1 + 2	33.125	0.560	0.82	8.30	2.45	51.80
	KPF (control)	119.375	2.340	5.54	2.70	0.52	17.30
Chlorella pyrenoidosa	CPo + LG = 1 + 7	93.125	0.675	1.62	2.00	1.05	12.60
	CPo + KP = 1 + 7	351.250	1.460	2.30	7.90	1.30	49.60
	ICIL + LG = 1 + 7	22.187	0.186	0.18	5.70	3.40	35.70
	ICIL = KP = 1 + 7	15.312	0.136	0.15	7.60	1.78	47.50
	ICIL + KP = 1 + 2	16.250	0.150	0.16	3.60	0.93	22.55
	KPF (control)	454.375	1.940	2.80	5.20	1.00	32.60

CPo = waste water from pig-farm; ICIL = waste water from dairy factory; LG = dam lake water; KP = Knop-Prigsheim's solution; KPF = Knop-Pringsheim-Felföldy's solution; N = nitrogen, P = phosphorus content of the cells (FABIAN et al., 1983)

reached the values of control only; both in multiplication (optical density) (Fig. 11) and in the amount of dry matter produced. The total protein content of dry matter was similar or even higher than that in the control (Table 1) (FABIAN et al., 1983). *Spirulina platensis* grew also well enough (in static cultures in Erlenmeyer flasks of 100, 300 or 1000 ml) in mixtures made of waste waters of brewery and dairy factory ameliorated with *Zarrouk*'s solution (in proportions of 1 + 1 + 2) as well as in mixtures of waste waters of dairy factory and pig-farm (at ratios between 5 : 1–9 : 1) enriched with *Zarrouk*'s solution salts in half dose. The amount of biomass produced was as high as 43–51%, although the pigment content was a little lower (BARNA et al., 1982). Massive cultures of this alga were also successful both in laboratory and in open, in *Zarrouk*'s solution (Fig. 12) (DRAGOŞ et al., 1982) as well as i ı mineral waters ("Hebe" or "Malnas") completed with N- and P-salts only (Table 2) (PÉTERFI et al., 1982).

Using waste waters (properly adjusted) as nutritive substrate for algae implies, evidently, many tempting perspectives (both experimental and biotechnological). Among others, the most alluring would perhaps be the wonderful bioaccumulation capacity of algae (i.e. their ancestral physiological characteristics) by which they are able to remove eutrophic (N, P) or toxic (Cu, Ni, Zn, Cd, Pb, Hg) elements or concentrate in their cells valuable materials from the very diluted aquatic environment.

Data gained from experiments concerning this subject proved that *Scenedesmus acutiformis* grown intensively (in parallelepiped plexiglass vessels) in nutrient mixtures based on waste water from brewery for 12–14 days was able to remove as much as 30–95% of N, reduce BOD_5 by 70–90% and improve some other qualities (e.g. colour, smell) of the initial liquid (BARNA, 1973, 1974; BARNA, NAGY-TÓTH, 1982). From nutrient liquids containing waste water of pharmaceutical works *Scenedesmus acutus*, though slow in growth, could reduce fixed residues by 90%, COD by 70%, and BOD_5 completely (PÉTERFI et al., 1978).

Bioaccumulation and removal of eutrophic as well as toxic substances by means of algae from the environment, respectively, though relevant (at least in the future (WURTZ, 1964)) looks (at present) a very difficult task, first of all, because of the specificity of nutrition despite the extended limits of tolerance, i.e. from optimum to toxic level) and of life condi-

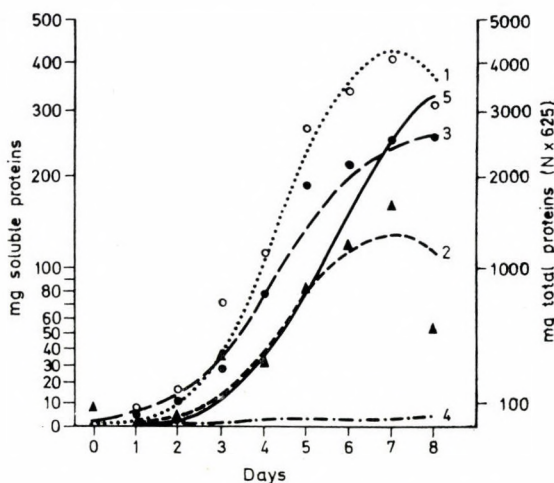



Fig. 12. Increase in protein content of *Spirulina platensis* grown in mass culture. 1 — total soluble proteins; 2 — phycobilinic proteins; 3 — soluble proteins without phycobilinic proteins; 4 — proteins in the medium; 5 — total proteins (N×625 mg/l) (DRAGOS et al., 1982)

Table 2

The nutritive value of enriched "Hebe" and "Malnas" mineral waters used for intensive (bubbled) batch cultures of Spirulina platensis

Measurements / Variants	Extinction	Dry weight mg/l	N mg/l	Total proteins % of d.w.	Bicarbonates, g/l	
					initial	final
Zarrouk (control)	1.419	1.302	164	78.72	10.169	3.381
75% Z + H	1.062	1.076	85.6	49.72	8.367	2.908
50% Z + H	1.560	1.144	123	67.19	6.384	2.612
N+P+HCO_3^-+H	0.963	1.140	62.2	34.10	11.049	2.719
75% Z + M	1.089	1.038	100.6	60.57	8.481	2.985
50% Z + M	1.695	1.594	170.4	66.81	6.091	3.439
N+P+HCO_3^-+M	0.747	0.524	10	11.92	12.053	4.095

Z = Zarrouk's solution; H = "Hebe" mineral water; M = "Malnas" mineral water; N, P, HCO_3^- = nitrogen, phosphorus and bicarbonate in amounts as in Z (PÉTERI et al. 1982)

tions as well concerning a profitable business, and then due to the huge and fluctuating amount of waters as well as to the compounds discharged in them. Results of experiments showed that mixtures of Tîrnava Mare river water (up- and down-stream of Copşa Mică, where it is fairly heavily loaded) and *Zehnder–Gorham*'s solution (in proportions between 20 + 1–0.5 + 1) assured (in static cultures) a rate of multiplication both for *Monoraphidium saxatile* and *Kirchneriella subcapitata* comparable to that of the control nutrient solution (Fig. 13), whereas mixtures of waste water of the Non-ferrous Metallurgical Factory a Copşa Mică (discharged in the river Tîrnava Mare) and the same Zehnder–Gorham's solution inhibited strongly the multiplication of both species, doubtless due to the metallic ions existing in the waste water (DRAGOŞ, 1980a). Waters of the river Tîrnava Mare (up-stream of Mediaş and down-stream of Copşa Mică), river Ampoi (up- and down-stream of Zlatna) and river Arieş (up- and down-stream of Baia de Arieş) without any enriching of essential nutrients had a very low trophic potential for *Scenedesmus acutus*, too. However, completed with *Tamiya* urea-EH's solution salts their nutritive value improved markedly. The Ampoi and Aries, river waters became more favourable than that of Tîrnava Mare (NAGY-TÓTH, BARNA, 1982). Dissolved in artificial nutrient solution (*Zehnder–Gorham*'s) it showed the toxicity level of Cu (22 μg/l) and of Ni (11 μg/l) for *Microcystis aeruginosa* and *Synechocystis minuscula* (both species grown in unialgal static cultures in Erlenmeyer flasks) (DRAGOŞ, 1980b), as well as those of Zn (50 μg/l), Cd and Pb (10 μg/l) for *Chlamydomonas intermedia* and *Scenedesmus acutus*. It was found that the bio-

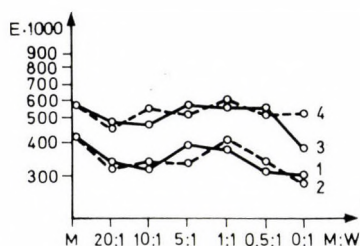



Fig. 13. Growth (E = extinction) of *Kirchneriella subcapitata* (1, 2) and *Monoraphidium saxatile* (3, 4) in static cultures in ZEHNDER-GORHAM's medium (M) and in its mixture with metal pickling wastes containing Tîrnava river water up-stream (1, 3) and down-stream (2, 4) of Copşa-Mică (DRAGOŞ, 1980a)

accumulation of these ions is positively correlated with the concentration; however, from less concentrated solutions living cells took up more than the dead ones (NAGY-TÓTH, BARNA, 1982).

Algological investigations covered in recent years a few caves, too. Some species and strains of blue-green and green algae have been isolated. In order to evidence some kind of presumably existing radiation which would promote biosyntheses simultaneous experiments were set up in laboratory and in cave. Measurements evidenced β-like radiations of cave rocks which, accordingly, were presumed to be possible energy sources promoting very weak anabolic processes (CRISTEA, 1983; CRISTEA, NAGY-TÓTH, 1983).

It is believed that the results of experiments carried out with waste waters broaden the fairly purposive special field of determination/or optimization of their phycotrophicity and could contr bute to the elaboration of larger research programs with multiple biotechnological and ecological reconstruction implications.

The experiments accomplished gave the chance to point out some interesting correlations between growth factors, functions and structures of thalli and cells as well. *Scenedesmus* species used to perform the majority of experiments surveyed in this article, are excellently suitable far finding out such cause-effect connections due to their highly pronounced plasticity (polymorphism) already evidenced in earlier studies (GRINTZESCO, 1902). As it is known, coenobia of this genus can be mono-, di-, tri- (seldom), tetra- (scene-) and multidesmoid (-celled). The proportion in a culture (population) of these forms varies accordingly to numerous environmental or experimental factors. Thus, *Scenedesmus quadrispina* (static cultures in test tubes) in media containing synthetic or natural growth substances (indoleacetic acid, gibberellic acid, or extract of vernalized and not-vernalized *Fleischmann* and Csanád wheat coleoptils, respectively) had a ratio of 1 : 29–1 : 6.64 between tetra- nd didesmoid coenobia; in aged cultures the value of proportion diminished, because of a decline in cell division. Without growth substances in aged cultures the cell dimensions became bigger since the cell division was, in this case, more inhibited (NAGY-TÓTH, 1964). *Scenedesmus acutus* (in intensive cultures, *Vladimirova–Semenenko*'s vessels) in suboptimal media based on waste waters (containing that of pharmaceutical works, too) appeared more frequently monodesmic fusiform or ellipsoid and ovoid as well (NAGY-TÓTH et al., 1976).

Based on cytophotometric measurements (cell by cell between 400–700 nm in every 5 nm with a Leitz-Ortholux MPE photometer microscope) of the absorption spectra of *Scenedesmus acutiformis* cells from a not-synchronized static culture population, 6 types of cells were distinguished, representing as many ontogenetic stages as related to their chlorophyll *a* and *b*- and carotenoids spectra, i.e. their chloroplast structures (NAGY-TÓTH, SORAN, 1979).

The large variability in habitats or in raw cultures of cell sizes of *Phormidium viscosum* grown in unialgal cultures (static and intensive, thermostated and thermoalternated as well) became considerably reduced (more homogeneous) which — as it was assumed — reflects a preference for one medium or another; the most favourable (of 10 experimented) were *Knop–Pringsheim–Felföldy*'s and *Watanabe*'s media (Fig. 14) (FABIAN et al., 1981).

Analysing the N-content simultaneously in nutrient solutions with different initial N-concentrations and in the cells of *Scenedesmus acutiformis* and *Spirulina platensis* grown in them, MITSCHERLICH's rule was validated for the nutrition of algae, too, as well as the converse correlation between N available in media and that bioconverted into cellular ones (bioconversion efficiency) (BARNA, NAGY-TÓTH, 1982).

On the basis of 6 *Scenedesmus* species/strains analysed (*Scenedesmus acutus*, *Sc. falcatus*, *Sc. obtusiusculus* I.D, III.C, and S, and *Sc.* sp. A) it was found that out of the many correlations which may exist among the life conditions, growth, productivity, total protein and pigment contents the converse correlation between the amount of photosynthesized dry matter and the ratio of chlorophyll *a*/*b* was the most probable (Fig. 15) (NAGY-TÓTH et al., 1980).

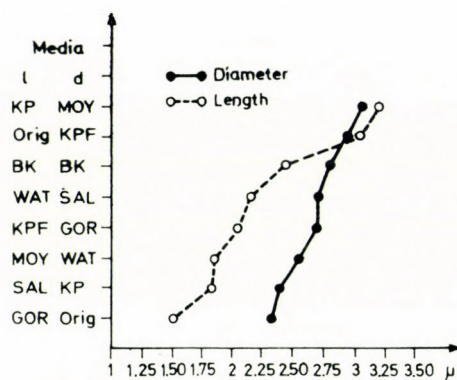



Fig. 14. The variation of cell size frequency of *Phormidium viscosum* depending on nutrient media (FABIAN et al., 1981)

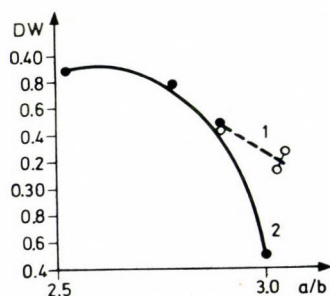



Fig. 15. A tentative correlation between the *a/b* chlorophyll ratio and the dry weight quantity (Dw g/l) by intensive cultures of *Scenedesmus acutiformis* (1) and *Sc. acutus* (2) (NAGY-TÓTH et al., 1980)

The survey of the Transylvanian phycophysiological researches would not be complete without mentioning, besides experimental endeavours, some accounts (about 30, with chapters on Treatise of Algology among them) based on literature data, which might contribute to a possible advance in algology.

REFERENCES

Barna, A. 1973: Forschungen bezüglich der intensiven Züchtung der Alge *Scenedesmus acutiformis* in Nährlösungen erzeugt mit Abwasser der Bierfabrik Cluj. — *Studia Univ Babeş-Bolyai*, ser. *Biol.* **2:** 51–59.

Barna, A. 1974: Cercetări privitoare la cultivarea intensivă a algei *Scenedesmus acutiformis* în soluţii nutritive pregătite cu apă reziduală de la fabrica de bere din Cluj (II). — *Studia Univ. Babeş-Bolyai*, ser. *Biol.* **1:** 67–71.

Barna, A. 1978: Nutriţia algelor cu referire la posibilitatea utilizării apelor reziduale industriale. — Teza Dr., Univ. Babeş-Bolyai, Cluj-Napoca, 1–190.

Barna, A., Nagy-Tóth, F. 1978: Despre efectele unor chelaţi asupra algei *Scenedesmus acutiformis*. — *Stud. Cercet. Biol.*, ser. *Biol. Veget.* **30:** 139–143.

Barna, A., Nagy-Tóth, F. 1980: Posibilităţi de utilizare a apelor termopoluante în cultivarea algelor. — *Stud. Cercet. Biol.*, ser. *Biol. Veget.* **32:** 47–51.

Barna, A., Nagy-Tóth, F. 1982: Contribution to the bioconversion efficiency of N-inorganic into N-organic by algae. — *Rev. Roum. Biol.*, ser. *Biol. Végét.* **27:** 29–35.

Barna, A., Nagy-Tóth, F., Bercea, V., Dragoş, N., Péterfi, L. S. 1982: Ape reziduale — posibile medii nutritive pentru *Spirulina platensis.* — Contrib. bot. (Cluj-Napoca), 201–208.

Barna, A., Nagy-Tóth, F., Bercea, V., Ştirban, M. 1977: Variaţia unor componenţi biochimici şi creşterea la specii de *Scenedesmus* cultivate în medii bazate pe ape reziduale. — *Studia Univ. Babeş-Bolyai*, ser. *Biol.* **3:** 31–38.

Barna, A., Nagy-Tóth, F., Péterfi, S. 1974: Influenţa pH-ului asupra creşterii algei *Scenedesmus acutiformis* în culturi intensive. — Contrib. bot. (Cluj-Napoca), 149–155.

Bercea, V., Tican, L., Dragoş, N., Oros, I. 1984: Phenol and syndets influence on the growth of *Monoraphidium contortum* (Thuret in Brébisson) Komárková-Legnerová green alga. — *Rev. Roum. Biol.*, ser. *Biol. Végét.* **29:** 45–51.

Bunt, J. S. 1968: The influence of inoculum size on the initiation of exponential growth by marine diatom. — *Z. Allg. Mikrobiol.* **8:** 289–292.

Cristea, V. 1983: La croissance et la multiplication des algues *Nostoc* sp. et *Scenedesmus acutus* Meyen dans le milieu cavernicole. — *Rev. Roum. Biol.*, ser. *Biol. Végét.* **28:** 87–91.

Cristea, V., Nagy-Tóth, F. 1983: Consideraţii asupra algelor din ecosistemele subterane. — Contrib. bot. (Cluj-Napoca), 17–23.

Dragoş, N. 1980a: Biotestarea apelor reziduale industriale deversate în Tîrnava cu ajutorul culturilor algale de laborator. — Contrib. bot. (Cluj-Napoca), 189–193.

Dragoş, N. 1980b: Efectul ionilor de Cu şi Ni asupra creşterii algelor albastre *Microcystis aeruginosa* Kütz. emend. Elenk. şi *Synechocystis minuscula* Woronich. — Contrib, bot. (Cluj-Napoca), 231–234.

Dragoş , N., Bercea, V., Péterfi, L. S. 1982: Cultura masivă a algei albastre *Spirulina platensis* (Gomont) Geitler în laborator şi în aer liber. — Simp. Naţ. Agric. Alim. Amb., Cluj-Napoca, 16–17 martie, 1982, Cluj-Napoca, 30–33.

Elis, R. J., Machlis, L. 1968: Nutrition of the green alga *Golenkinia.* — *Amer. J. Bot.* **55:** 590–599.

Fabian, A., Nagy-Tóth, F., Barna, A., Rácz-Bélteki, E. 1981: About the morphological and physiological characteristics of the blue-green alga *Phormidium viscosum* Lemm. — *Rev. Roum. Biol.*, ser. *Viol. Végét.* **26:** 133–140.

Fabian, A., Nagy-Tóth, F., Barna, A., Coman-Mitrea, A. 1983: Quelques caractéristiques de la croissance des algues en conditions nutritionelles assurées par les eaux résiduelles. — *Studia Univ. Babeş-Bolyai*, ser. *Biol.* **28:** 30–39.

George, E. A. 1978: The culture collection point of view. — *Mitt. Int. Verein. Limnol.* **21:** 31–33.

Grintzesco, J. 1902: Recherches expétimentales sur la morphologie et la physiologie de *Scenedesmus acutus* Meyen. — *Bull. Herb.* Boiss., 2e sér., **3:** 217–288.

Grintzesco, J. 1930: Les cultures pures et leur importance pour l'étude des algues, des schizophytes et des champignons. — Premier Congrès National des Naturalistes de Roumanie, 18–21 Avril 1928, Ed. Soc. Ştiinţe, Cluj, 171–173.

Hindák, F. 1970: Biomass production of filamentous green algae (*Ulotrichales*) in cultures. — *Algol. Stud.* **1:** 77–109.

Hutner, S. H. 1972: Inorganic nuctrition. —*Annu. Rev. Microbiol.* **26:** 313–338.

Lankford, C. E., Walker, J. R., Reeves, J. B., Nabbut, N. H., Byers, B. R., Jones, R.J. 1966: Inoculum-dependent division lag of *Bacillus* cultures and its relation to an endogenous factor(s) („schizokinen). — *J. Bacteriol.* **91:** 1070–1079.

Lorenzen, H. 1974: Problems of time measuring in *Chlorella.* — *Colloq. Int. C.N.R.S.* (*Paris*) **240:** 41–46.

Lorenzen, H., Schleif, J. 1966: Zur Bedeutung kürzest möglichen Generationsdauer in Synchronkulturen von *Chlorella.* — *Flora* (*Jena*), Abt. A, **156:** 673–683.

Marton, A. 1973a: Acţiunea unor substanţe bactericide şi fungicide asupra algei verzi *Stichococcus bacillaris.* — *Stud. Cercet. Biol.*, ser. *Bot.* **25:** 79–85.

Marton, A. 1973b: Cercetări privind acţiunea unor substanţe antibiotice şi antiseptice asupra creşterii şi diviziunii algei *Stichococcus bacillaris.* — *Stud. Cercet. Biol.*, ser. *Bot.* **25:** 341–346.

Marton, A. 1975: Forschungen über die intensive Kultur der Grünalge *Stichococcus bacillaris Nägeli* in verschiedenen Nährmedien. — *Rev. Roum. Biol.* **20:** 49–53.

Marton, A., Cachiţă-Cosma, D. 1974a: Acţiunea procainei asupra algei verzi Stichococcus bacillaris în diferite condiţii de cultivare. — *Stud. Cercet. Biol.* **26:** 179–182.

Marton, A., Cachiţă-Cosma, D., Popovici, G. 1974b: Acţiunea procainei asupra creşterii şi dezvoltării algei Stichococcus bacillaris. — *Stud. Cercet. Biol.* **26:** 47–51.

Marton, A., Chindriş, E. 1974: Acţiunea biologică a unor compuşi heterociclici. I. Acţiunea mitodepresivă a unor 2-aril-4-clorometil-oxazoli asupra algei verzi Stichococcus bacillaris Nägeli. — *Clujul Medical* **47:** 387–397.
Nagy-Tóth, F., 1964: Contribuţii la cunoasterea variaţiei talurilor de Scenedesmus quadrispina Chod. sub influenţa substanţelor stimulatoare de creştere. — *Contrib. Bot.* (Cluj), 321–328.
Nagy-Tóth, F. 1972: Cercetări privitoare la cultivarea intensivă a unor alge verzi. — Teza Dr., Univ. Babeş-Bolyai, Cluj, 1–333.
Nagy-Tóth, F., Barna, A. 1982: Analiza algofizologică a unor ape metalopoluate. — *Stud. Cercet. Biol.*, ser. *Biol. Veget.* **2:** 134–139.
Nagy-Tóth, F., Barna, A., Péterfi, L. S., Dragoş, N., Bercea, V. 1982: Creşterea şi compoziţia algei *Spirulina platensis* la proporţii diferite de C, N, P. *Contrib. Bot.* (Cluj-Napoca), 209–215.
Nagy-Tóth, F., Barna, A., Ştirban, M., Bercea, V. 1976: Cercetări privitoare la cultivarea intensivă a algei Scenedesmus acutus în soluţii nutritive pregătite cu ape reziduale industriale din Municipiul Cluj-Napoca (III). *Contrib. Bot.*, 227–231.
Nagy-Tóth, F., Bercea, V., Barna, A., Ştirban, M. (1980): The dynamics of photosynthetic pigments and the productivity of some *Scenedesmus* species. — *Rev. Roum. Biol., ser. Biol. Végét.* **25:** 21–43.
Nagy-Tóth, F., Péterfi, S., Barna, A. 1974: Problema schizokinineloer la alge (I). — *Studia Univ. Babeş-Bolyai*, ser. *Biol.* **2,** 51–58.
Nagy-Tóth, F., Soran, V., 1979: Data concerning the absorption spectrum of Scenedesmus acutiformis intact cells. — *Rev. Roum. Biol., ser. Biol. Végét.* **24:** 33–37.
Péterfi, L. S., Bercea, V., Dragoş, N., Veres, M. 1982: Utilizarea apelor minerale în cultura masivă a algei albastre *Spirulina platensis* (Gom.) Geitler. — *Simp. Naţ. Agric. Alim. Amb., Cluj-Napoca* 16–17 martie, 1982, Cluj-Napoca, 33–35.
Péterfi, S. 1967: Cercetări asupra algelor în culturi pure în Republica Socialistă România. *Contrib Bot.*, 281–286.
Péterfi, S., Barna, A., Nagy-Tóth, F. 1975: Die Züchtung der Alge Scenedesmus acutiformis auf aus Abwasser und Mineralwasser zusammengesetzten Media. In: *Nečas*, J. (pod red.): Izuch. Intesivnoi Kul'tury Vodoroslei II. Dokl. X. Koord. Sovesch. SEV, Třeboň, 1975, Třeboň, 121–129.
Péterfi, S., Barna, A., Nagy-Tóth, F., Ştirban, M., Bercea, V. 1977: Optimierung des Nährwertes einiger Abwässer für die Algenzüchtung. — *Rev. Roum. Biol.*, ser. *Biol. Végét.* **33:** 99–105.
Péterfi, S., Marton, A. 1977: Relations between some green filamentous algae and the pH of their natural or artificial growth medium. — *Studia Univ. Babeş-Bolyai*, ser. *Biol.* **1:** 20–27.
Péterfi, S., Nagy-Tóth, F. 1979: The influence of some inorganic complexes upon the algal growth. In: *Sălăgeanu, N., Codreanu, R.* (coords.): The Results of the Romanian Researches Carried Out in the Framework of the International Biological Programme, Ed. Acad. R.S.R., Bucureşti, 86–96.
Péterfi, S., Nagy-Tóth, F., Barna, A. 1969: Der Wachstumsverlauf von Scenedesmus acutiformis in periodisch verdünnten intensiven Kulturen. — *Studia Univ. Babeş-Bolyai*, ser. *Biol.* **1:** 73–82.
Péterfi, S., Nagy-Tóth, F., Barna, A. 1975: Efectul unor microelemente în solutii nutritive complete asupra culturilor intensive de alge. — *Studia Univ. Babeş-Bolyai*, ser. *Biol.* **20:**. 17–23.
Péterfi, S., Nagy-Tóth, F., Barna, A. 1976: Some results of the researches of Cluj concerning the nutrition of algae. — *Acta Bot. Acad. Sci.* Hung. **22:** 149–161.
Péterfi, S., Nagy-Tóth, F., Narna, A., Ştirban, M., Bercea, V. 1978: Some metabolic characteristics of Scenedesmus acutus cultivated in media prepared from waste waters. — *Rev. Roum. Biol.*, ser. *Biol. Végét.* **23:** 45–53.
Pringsheim, E. G. 1954: *Algenreinkulturen.* Fischer-Verlag, Jena, 1–98.
Provasoli, L. 1958: Nutrition and ecology of protozoa and algae. — *Rev. Microbiol.* **12:** 279–308.
Skulberg, O. M. 1966: Algal cultures as a mean to assess the fertilizing influence of pollution. — Third Int. Conf. Water Pollut. Res., Munich (Germany), 1–15.
Tămas, M., Marton, A., Chindris, E. 1975: Acţiunea biologică a unor compuşi heterociclici. II. Modificări calitative ale pigmenţilor asimilatori din alga verde Stichococcus bacillaris Nägeli sub acţiunea unor 2-aril-clormetil-oxazoli. — *Clujul Medical* **48:** 65–68.
Weiss, C. 1971: Inter-laboratory precision test. Nat. Eutroph. Res. Program, Environm,. Prot: Agency, Univ. North Carolina, Chappel Hill, 1–70.
Wurtz, A. G. 1964: Some problems remaining in algae culturing. In: Jackson, D. F. (ed.): *Algae and Man.* Plenum Press, New York, 120–137.

Acta Botanica Hungarica 33 (3—4), pp. 371—376 (1987)

THREE MORPHOLOGICALLY DIFFERENT ISOLATES OF *TRICHODERMA HAMATUM* FROM HUNGARY

L. VAJNA[1] and ILONA GARAMVÖLGYI MRS. APONYI[2]

[1] PLANT PROTECTION INSTITUTE OF THE HUNGARIAN ACADEMY OF SCIENCES, BUDAPEST
[2] CENTRE FOR PLANT PROTECTION AND AGROCHEMISTRY OF THE MINISTRY OF AGRICULTURE AND FOOD, BUDAPEST

(Received: 15 February 1987)

Three different Hungarian isolates of *Trichoderma hamatum* were studied. Significant differences were established in the form and size of phialospores and in the appearance of the conidial area. The colour of the conidial area depends on the degree of the development of the steril hyphal elongations. Isolate Tha-1 should be considered as a typical representative of *T. hamatum* species.

Introduction

Trichoderma hamatum (Bon.) Bain. according to RIFAI (1969) is a very widely distributed fungus, known in Europe, North America, Asia and Australia. Investigations carried out during the last fifteen years have demonstrated that this species is important as a hyperparasitic fungus (ELAD *et al.* 1983) and an active producer of non-volatile antibiotics (DENNIS and WEBSTER 1971), and as a soil inhabiting fungus can play an important role in the process of decomposing of organic substrates.

T. hamatum according to the revision of the genus *Trichoderma* (RIFAI 1969) is morphologically probably the most heterogenous species. As it was stated by RIFAI (1969): "*When a more exact and more elaborate system of classification of the genus Trichoderma is attempted there is no doubt that this heterogenous species aggregate will be the first to be split into several smaller entities.*"

No data are available concerning the occurrence of this species in Hungary. Moreover significant morphological differences between these isolates were observed. At the same time two of the three isolates (Tha-1 and Tha-2) are highly active antagonists producing antifungal antibiotics and they are active mycoparasites, too. Therefore they can be used potentially as biocontrol organisms.

Material and Methods

The first isolate of *T. hamatum* (Tha-1) was isolated from soil of carnation in 1983 near the city Győr by I. GARAMVÖLGYI. The second one (Tha-2) isolated by L. VAJNA from surface of sterilized sclerotia of *Sclerotinia sclerotiorum* collected in 1983 in the Fejér county, and the third one (Tha-3) isolated by L. VAJNA from a ripening sunflower plant in 1984 in the Fejér county. Cultures of all the three isolates are deposited in the culture collection of the Plant Protection Institute (Budapest).

Monoconidial cultures of these three isolates were grown on PDA in Petri dishes with diameter of 10 cm, in three replicates. The pH of the medium was 7.0. Centrally inoculated plates were incubated at 27 °C in a phytotrone with 12 hours of lightening daily. The intensity of radial growth was determined by daily measurement of diameters of the colonies.

During the incubation period the characteristics of morphology of colonies were described. Morphological features of the three isolates were studied by light microscopy according to the suggestions of RIFAI (1969).

Characteristics of the isolate Tha-1

Colonies grow rather slowly, 14 mm daily. They are watery white and without aerial hyphae. The conidial area appears at the 4–5th day as a ring at the edge of the Petri dish (Fig. 1). Discolouration of the medium does not take place. The conidiophores form very compact tufts. Secondary type of conidiophores (koningii-type) as usual is absent. Tufts are at first white, later velvety greyish-green. This appearance of tufts is due to the presence of well-developed septate steril hyphal elongations (Fig. 2). The phialospores are pale-green, ellip-

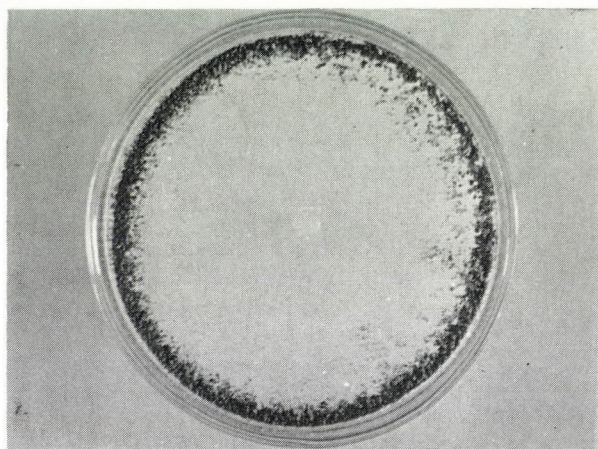



Fig. 1. One week old colony of the isolate Tha-1

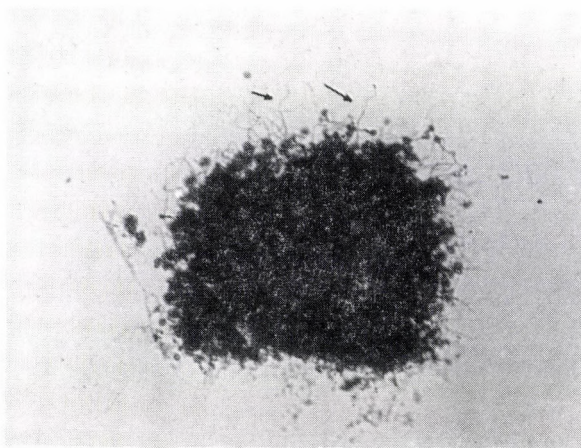



Fig. 2. Well-developed steril hyphal elongations of isolate Tha-1, ensuring velvety appearance to tufts

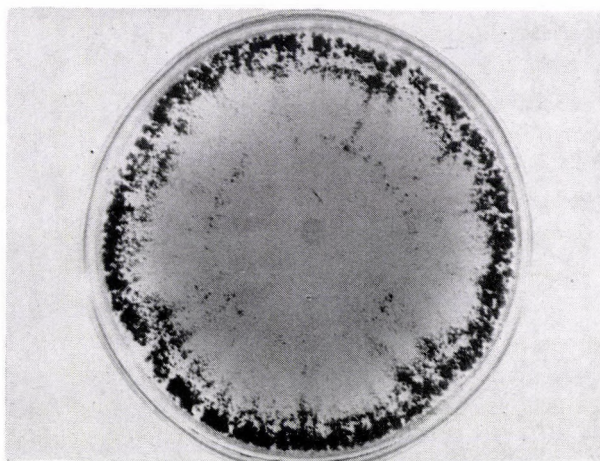



Fig. 3. One week old colony of the isolate Tha-2

soidal, subcylindrical, rounded at the apices and measure 3.6–4.8 × 2.4–2.8 μm (average: 4.1 × 2.5 μm) (Fig. 6a). Formation of roundish apical or intercalary chlamydospores in the substrate is common. This isolate does not produce any characteristic odor.

Characteristics of the isolate Tha-2

Colonies grow slowly, 9.2 mm daily, watery white almost without aerial hyphae. The conidial area appears between the 48–72 hours of incubation in ring-like zones, first zone formed close to the centre of plates, later three more zones are forming regularly toward the edge of Petri dishes (Fig. 3). The conidiophores form rather loose tufts which are often united. Irregular, atypical, sometimes koningii-type conidiophores are formed between the distinct zones of tufts. Tufts are at first white, later whitish-green, finally dark-green. There is no velvety appearance of the conidial fructification. Formation of steril hyphal elongations is common in tufts (Fig. 4). The phialospores are pale-green, obovoid, rounded at the apices and attenuated slightly below into a truncate base and measure 2.8–3.6 × 2.4–3.2 μm, average 3.2 × 2.7 μm (Fig. 6b). Formation of chlamydospores was not observed. This isolate does not produce characteristic odour.

Characteristics of the isolate Tha-3

Radial growth of colonies is rather slow, 15 mm daily. The colonies are at first watery white with very poor formation of aerial hyphae, which can be seen only microscopically. Discolouration of the medium does not take place. The first conidial area appears very early, after 24–30 hours of incubation at the centre of the plates (Fig. 5). Tufts are very small and rather loose, they form wide ring-like zones. Formation of some small tufts and atypical, or simple conidiophores were observed in the areas between zones. Tufts are at first white, later whitish-green, finally dark-green. Formation of typical hyphal elongations was observed in tufts. The phialospores are obovoid, rounded at the apices, attenuated slightly below into

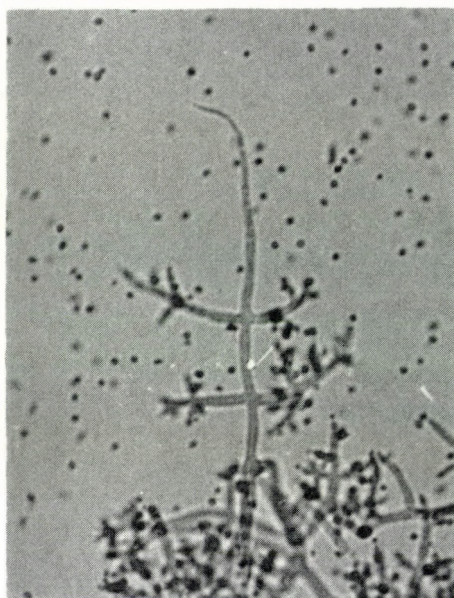



Fig. 4. Steril septate hyphal elongation on the conidiophore of the isolate Tha-2

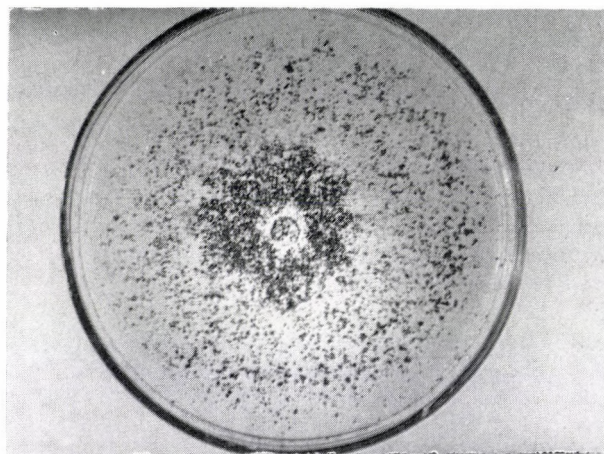
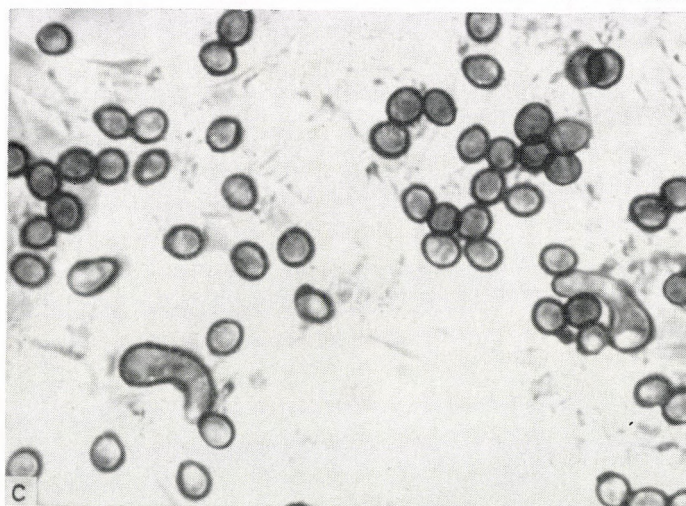
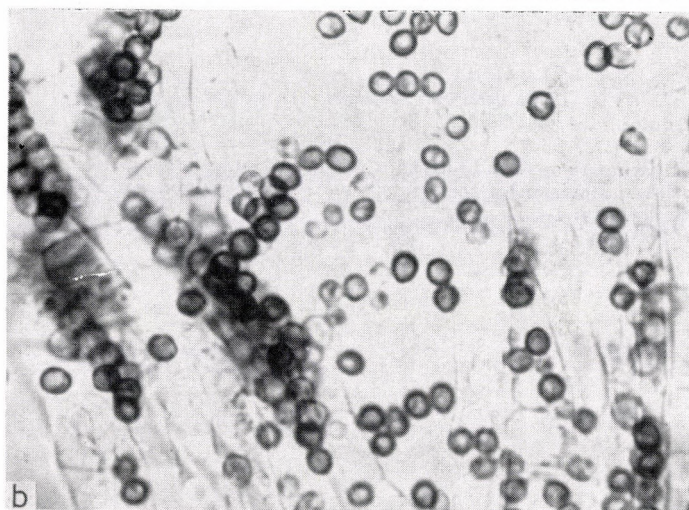
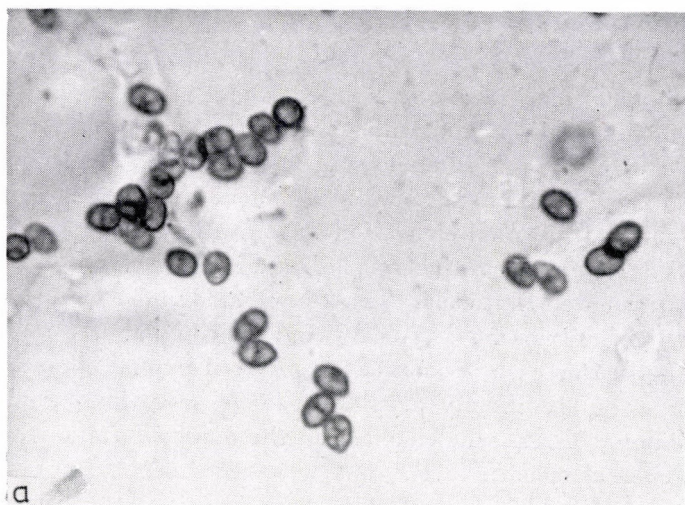



Fig. 5. One week old colony of the isolate Tha-3

a truncate base and measure 3.6–4.8 × 3.2–4 μm, average 4.2 × 3.7 μm (Fig. 6c). Formation of globose, intercalary or terminal chlamydospores in the substrate is common.

All the three isolates have phialides in tufts characteristic to the species, their arrangement and the morphological characteristics of conidiophores are the same as described by RIFAI (1969).

→

Fig. 6. Conidia of the *T. hamatum* isolates, — a) Tha-1, b) Tha-2, c) Tha-3 — (The magnification of the three pictures in the same)

Discussion

Three isolates of *Trichoderma* sp. according to the morphology of conidiophores, phialides, their arrangement belong to the species of *T. hamatum*.

There are important differences in the form and size of phialospores. The colour of the conidial area of colonies depends on the degree of the development of the steril hyphal elongations. Isolate Tha-1 is a typical representative of *T. hamatum* according to the description given by RIFAI (1969).

It must be noted that isolate Tha-2 incubated under the same conditions but without light did not form typical tufts, the conidial area is similar to the koningii-type. In this case the formation of steril hyphal elongations is rare, the conidiophores are mostly atypical. This observation is in accordance with the opinion of RIFAI who emphasized the doubtful value of steril hyphal elongations even at specific level.

REFERENCES

Dennis, C., Webster, J. 1971: Antagonistic properties of species groups of *Trichoderma*. I. Production of non-volatile antibiotics. *Trans. Br. Mycol. Soc.*, **57:** 25–39.

Elad, Y., Rina Barak, I. Chet, Y. Henis 1983: Ultrastructural studies of the interaction between *Trichoderma* spp. and plant pathogenic fungi. *Phytopath. Zeitschr.*, **107:** 168–175.

Rifai, M. A. 1969: A Revision of the Genus *Trichoderma*. *Mycol. Papers, CMI Kew*, Surrey, England, No. **116:** 1–56.

Acta Botanica Hungarica 33 (3—4), pp. 377—385 (1987)

PHYTOECDYSTEROIDS IN SOME SPECIES OF CARYOPHYLLACEAE AND CHENOPODIACEAE

BÁTHORI, M.[1], MÁTHÉ, I. JR[2], SOLYMOSI, P.[3], SZENDREI, K.[1]

[1] DEPARTMENT OF PHARMACOGNOSY, UNIVERSITY MEDICAL SCHOOL SZEGED, H-6701 SZEGED, P.O.B. 121

[2] INSTITUTE OF ECOLOGY AND BOTANY OF THE HUNGARIAN ACADEMY OF SCIENCES, VÁCRÁTÓT, H-2163

[3] RESEARCH INSTITUTE OF PLANT PROTECTION OF THE HUNGARIAN ACADEMY OF SCIENCES, BUDAPEST, H-1022 HERMAN OTTÓ u. 15.

(Received: 21 November 1986)

In the course of studying the occurrence of phytoecdysteroids 26 of 105 species of the family Caryophyllaceae and 19 of 38 chenopodiaceous species were found to contain ecdysteroids. On the basis of isolations and chromatographic examinations carried out so far 20-hydroxyecdysone (β-ecdysone) proved to be the main ecdysteroid component in each case. Of the associate compounds 2-deoxy derivatives seem to occur regularly in *Silene* species of the family Caryophyllaceae. Studies of several species belonging to further 5 families of the Centrospermae suggest that the occurrence of ecdysteroids is characteristic of certain genera of the family Amaranthaceae in addition to the two families above. The frequent occurrence of ecdysteroids is remarkable in the species *Silene*, *Melandrium* and *Lychnis* which belong to the subfamily Silenoideae of the family Caryophyllaceae.

Introduction

The arrangement of taxa in the earlier plant systems set up on the basis of morphological characters has left many questions open which can hardly be answered on a traditional, merely morphological basis. Among the modern approaches the consideration of chemical features together with other characteristics may do good service in deciding debated questions. For methodological reasons a comparative evaluation first of all of compounds of low and medium molecular weight seems to be expedient.

In the classification of Centrospermae the relationship between the two families of high species number, Caryophyllaceae and Chenopodiaceae, has been an accepted fact for a long time, however, the opinions differ regarding the degree of relationship. So in ENGLER's system the two families belong to two suborders (1. and 4.) (ENGLER 1964), according to WETTSTEIN they form the 1. and 10. families of the 14. order of Dicotyledons (WETTSTEIN 1935), while at HUTCHINSON (1959) they are found in two orders (62. and 64.). In GROSSHEIM's system (1928) they are families of the order of Centrospermae (section Centrospermalia), while according to Soó (1965) they are the families 5. and 6. of the order 30. of section 4.

In the systemization of the Centrospermae the discovery was an important momentum (MABRY 1963) that in the families belonging here — except the Caryophyllaceae, and the Molluginaceae which some authors consider as a separate family — the betalaines (betacyanine and betaxanthine alkaloids) occur as colouring materials replacing the anthocyanines, the generally known colouring materials of the flora including the two families mentioned above as exceptions. In spite of this important difference there are controversies concerning the degree of relationship. TAKHTAJAN (1973) insists that the two families (162. and 166.) belong to the same order, the order of Caryophyllales, and so do CRONQUIST (1968) and DAHLGREN

(1977). BEHNKE (1971), on the other hand, differentiates two orders — the Caryophyllales and the Chenopodiales — within the Caryophyllidae subclass, that is, he regards the difference in betalain occurrence as determinative at the level of order, too. In his system beside the colouring matters of plants the electron microscopic differences (TEM) in the protein- and starch accumulation of sieve tubes are also taken into consideration. Accordingly, the families Caryophyllaceae and Molluginaceae belong to the order of Caryophyllales, while the order Chenopodiales includes the following families: Phytolaccaceae, Stegnospermaceae, Nyctaginaceae, Didiereaceae, Cactaceae, Aizoaceae, Portulacaceae, Basellaceae, Chenopodiaceae, Amaranthaceae.

Beside the presence or absence of betalain alkaloids a range of other chemical information is also available, such as e.g. data on flavonoids, sugar derivatives, saponines, etc. (HEGNAUER 1964), which when taken into consideration may serve as an additional material to minute classifications between and within the families. Evaluating the occurrence of ecdysteroids, a compound biochemically closely related with the saponines, discovered in the fauna as a moulting hormone, may serve a similar purpose.

Since the discovery of ecdysteroids occurring in the flora (1966) many compounds of this type have been isolated. On the basis of the data obtained so far they seem to be present in taxa as distant from one another as, e.g. the Gymnospermae and the Angiospremae; in the latter in species of families belonging to different subclasses. In spite of their wide distribution their appearance is far from being as general as, e.g. the appearance of sitosterols, which holds out hopes of using these compounds for taxonomic purposes.

Table 1

Occurrence of ecdysteroids in the family Caryophyllaceae

Genus	Number of samples	Number of species examined / ecdysteroid- — containing
Silenoideae subfamily		
Agrostemma	2	2/0
Viscaria	2	1/0
Silene	144	55/22
Lychnis	4	2/2
Melandrium	11	7/2
Cucubalus	2	1/0
Gypsophila	8	5/0
Tunica	6	2/0
Vaccaria	2	1/0
Dianthus	16	6/0
Saponaria	1	1/0
Alsinoideae subfamily		
Stellaria	3	3/0
Cerastium	9	9/0
Minuartia	4	4/0
Spergula	2	2/0
Scleranthus	3	1/0
Paronychoideae subfamily		
Herniaria	3	3/0
		105/26

Table 2

Occurrence of ecdysteroids in the family Chenopodiaceae

Genus	Number of samples	Number of species examined / ecdysteroid-— containing
Cyclolobeae subfamily		
Beta	4	1/1
Chenopodium	57	21/13
Spinacia	5	1/1
Atriplex	19	9/3
Kochia	2	2/1
Corispermum	1	1/0
Spirolobeae subfamily		
Suaeda	2	2/0
Salsola	3	1/0
		38/19

The results of our systematic study aimed primarily at seeking out species with high ecdysteroid contents offer a possibility for the chemosystematic evaluation of the material examined as well.

Material and method

The plant material used for the screening tests was collected partly on collecting trips all over the country, partly from the trial grounds of the Institute of Ecology and Botany of the Hungarian Academy of Sciences. Freshly collected (10 g) and/or dried 5 g) plant samples were mixed in shaker with 100 ml methanol for 3 minutes. The methanolic extracts were filtered then distilled in vacuum, and the dry residue was dissolved in 10 ml methanol. The methanol solution was subjected to qualitative and semi-quantitative analysis by thin layer chromatography together with 20-hydroxyecdysone. (Kieselgel GF_{254}, mobil phase: dichloromethane-ethanol (4 : 1); ethyl acetate-methanol-ammonium hydroxide (85 : 10 : 5); chloroform-methanol-acetone (6 : 2 : 1).)

The chromatograms were evaluated first in UV-light at 254 nm wavelength, then — after sprayed with vanillin-sulphuric acid — in sunlight and in UV-light at 360 nm. In case of a sample found positive RIA measuring was also carried out.

In the radioimmune tests either anti-polypodine B antiserum was used, which is equally sensitive to ecdysone and 20-hydroxyecdysone, or (H-21-B)-ecdysone sensitive antiserum. Identical quantities (1.4 ml) of the plant extract were measured in Eppendorf tubes and dried with tritium labelled ecdysone under nitrogen stream, then with 100 ml 1% anti-polypodine B antiserum (dissolved in RIA buffer) added, they were incubated at 38 °C for 30 minutes. The bound and free radioactive substances were separated by precipitation with ammonium sulphate (Maroy *et al.* 1977).

For some species the results obtained by preliminary examinations were checked by preparative processing. These results as well as of the UV-, IR-, weight- and NMR spectroscopy examinations of the structures of compounds obtained in the course of processing were published earlier (Báthori *et al.* 1981, 1982, 1984, 1986, 1986a, 1986b).

Results

The results of chromatographic examinations of aboveground plant samples mostly collected at the stage of flowering are shown in Tables 1 and 2. In Table 1 the number of the caryophyllaceous species examined and of those found positive, i.e. containing ecdysteroid are indicated by genus. The table also includes the number of samples without specifications.

Table 3

Ecdysteroids isolated from species of Caryophyllaceae and Chenopodiaceae

Species	Ecdysteroid	References
Caryophyllaceae (*Silene* genus)		
Silene brahuica Boiss.	20-hydroxyecdysone viticosterone E silenoside A, B, C, D, E 5.20-dihydroxyecdysone (polypodine B) ecdysone-22-sulphate integristerone A (1.20-dihydroxyecdysone) 2-deoxyecdysone 2-deoxy-20-hydroxyecdysone	SAATOV *et al.* 1981, 1982, 1982a, 1984, 1986.
Silene praemixta M. Pop.	20-hydroxyecdysone 2-deoxyecdysone 2-deoxy-20-hydroxyecdysone silenosterone praemixisterone 2-deoxy-20-hydroxyecdysone-3-acetate ecdysone viticosterone E	SAATOV *et al.* 1979, 1979a, 1985
Silene longicalycina Kom.	20-hydroxyecdysone	
Silene Wallichiana Klotzsch.	20-hydroxyecdysone	
Silene latifolia (Mill.) Rendle	20-hydroxyecdysone 2-deoxyecdysone 2-deoxy-20-hydroxyecdysone	
Silene nutans L.	22-deoxy-20-hydroxyecdysone 20-hydroxyecdysone 5,20-dihydroxyecdysone (polypodine B) 1,20-dihydroxyecdysone (integristerone A) nusilsterone	BALTAEV *et al.* 1984, 1985, 1986. BÁTHORI et al. 1986 b
Silene scabrifolia Kom.	20-hydroxyecdysone-22-O-benzoate 2-deoxyecdysone 20-hydroxyecdysone	SAATOV *et al.* 1986.
Silene otites (L.) Wib. ssp. hungarica Wrigley	20-hydroxyecdysone 20-hydroxyecdysone-22-acetate 2-deoxy-20-hydroxyecdysone 2-deoxyecdysone 20,26-dihydroxyecdysone 2-deoxyecdysone-22-acetate 2-deoxy-20-hydroxyecdysone-22-acetate 1,20-dihydroxyecdysone (integristerone A)	BÁTHORI *et al.* 1986, 1986a.
Lychnis flos-cuculi L.	20-hydroxyecdysone 5,20-dihydroxyecdysone (polypodine B) 22-deoxy-20-hydroxyecdysone	BÁTHORI *et al.* (in press.)

Table 3 (continued)

Species	Ecdysteroid	References
Lychnis flos-cuculi L.	viticosterone E rubrosterone 1,20-dihydroxyecdysone (integristerone A)	
Chenopodiaceae		
Chenopodium album L.	20-hydroxyecdysone 5,20-dihydroxyecdysone 20-hydroxy-24-methylene-ecdysone (24/28/-dehydromakisterone A)	Báthori *et al.* 1981, 1984.
Chenopodium bonus-Henricus L.	20-hydroxyecdysone 20-hydroxy-24-methylecdysone (makisterone A)	Báthori *et al.* 1982, 1984.
Spinacia oleracea L.	5,20-dihydroxyecdysone (polypodine B) 20-hydroxyecdysone 20-hydroxy-24-methylene-ecdysone (24/28/-dehydromakisterone A)	Báthori *et al.* 1982, 1984.

According to our data the species *Silene*, *Lychnis*, and *Melandrium* from the subfamily Silenoideae proved to contain ecdysteroids in the first place, while in the samples (species) belonging to the other genera ecdysteroids were not found. The most remarkable result was obtained in the case of the genus *Silene*, where 22 of the 55 species examined proved positive. This means about 40 percent of the species examined. In the genus *Lychnis* the occurrence of ecdysteroids was 100 percent, though it must be added that this result is based on a merely 4 samples of 2 species.

Table 2 presents the data of the family Chenopodiaceae similarly indicating the number of species examined and found positive, respectively. The number of samples per genus is also given. The table reveals that the species of genera belonging to the Betoideae and Chenopodioideae tribes of the subfamily Cyclolobeae were found to contain ecdysteroids, and out of them — in accordance with our earlier publications (Báthori 1981, 1982, 1984) — it is in the *Chenopodium* and *Atriplex* species that the presence of ecdysteroids is frequent. These compounds were pointed out in 48 percent of those examined by us.

By thin layer chromatography 20-hydroxyecdysone, i.e. β-ecdysone was found to be present as main component in every species proved positive in both families. Beside it there are many other components. However, in an interesting way ecdysone itself (α-ecdysone) could not be detected in any of the samples, moreover, even in the course of preparative separations carried out with some species its presence could not be demonstrated. In Table 3 ecdysteroids isolated by us and by Soviet authors from some species of the families Caryophyllaceae and Chenopodiaceae are shown. Accordingly, beside 20-hydroxyecdysone, always present as the main component, 2-deoxy derivatives were found in several *Silene* species, in opposition to the chenopodiaceous species from which they were absent. From *Silene otites** 2-deoxy-ecdysone and 2-deoxy-20-hydroxyecdysone could even be isolated and their structures defined (Báthori 1986). It should be noted that these compounds were first isolated from silkworms and were found to play an important role in the process of sexual maturing

* More accurately *Silene otites* ssp. *hungarica* Wrigley (editor).

Table 4

Results of quantitative examinations of ecdysteroid contents

Species	Ecdysteroid content, % (fresh plant)
Chenopodiaceae	
Ch. album L.	0.004–0.02
Ch. quinoa L.	0.001–0.03
Ch. bonus-Henricus L.	0.0005–0.001
Ch. giganteum D. Don.	0.006–0.06
Spinacia oleracea L.	0.001–0.02
Caryophyllaceae	
Silene otites (L.) Wib. ssp. *hungarica* Wrigley	0.2–0.1
Silene nutans L.	0.1

and ovulation, and to be intermediate products of the biosynthesis of 20-hydroxyecdysone and ecdysone (ABUBAKIROV 1981, OHNISHI *et al.* 1977, 1981, IKEKAWA 1983). In plants these compounds were first discovered in *Blechnum* species of the Polypodiaceae. Their presence in some *Silene* species is confirmed by examinations carried out by Soviet authors parallel with us (ABUBAKIROV 1981).

Similarly remarkable is the detection of 20,26-dihydroxyecdysone and 20-hydroxyecdysone-22-acetate in *Silene otites*. It was the first time that the latter could be isolated from the plants.

As for the Chenopodiaceae species included in Table 3 it should be mentioned that ecdysteroids containing methyl or methylene group at C24: the makisterone A and the $\Delta^{24(28)}$-dehydromakisterone A also appear there in opposition to the Caryophyllaceae species.

Data on the quantity of ecdysteroids, based first of all on RIA measurements, are available as yet for several species of Chenopodiaceae and Caryophyllaceae of particular interest. According to our results the total ecdysteroid content is 0.0005–0.2 percent in fresh plants (Table 4). On the basis of the data of Table 4 the *Silene* species analysed in some detail appear to be more favourable sources of ecdysteroid than the representatives of the other family. A particularly remarkable ecdysteroid accumulation is reported by Soviet authors — a 20-hydroxyecdysone content of 0.65 percent in *Silene praemixta* (ABUBAKIROV 1981).

Table 5

Supplementary data on the occurrence of ecdysteroids in families of Centrospermae

Family	Number of species examined / positive
Nyctaginaceae	3/0
Phytolaccaceae	1/0
Portulacaceae	2/0
Aizoaceae	1/0
Amaranthaceae	12/2

Table 5 contains data on representatives of randomly examined centrospermous families. Reliable information of representative level concerning the occurrence of ecdysteroids could only be obtained for the family Amaranthaceae. Our own results and data from the literature equally show that the *Achyranthes* species are the ones in which ecdysteroids could be detected.

We analysed *Mirabilis dichotoma* L., *M. jalapa* L. and *M. nyctaginea* (Mich.) McMillan from the family Nyctaginaceae; *Phytolacca clavigera* L. from the Phytolaccaceae; *Portulaca oleracea* L. and *P. grandiflora* Hooker from the Portulacaceae; *Tetragonia tetragonoides* (Pallas) O. Ktze from the family Aizoaceae and found all these species negative. Since in comparison to the number of species belonging to the families in Table 5 data are available only for a small number of species, and so general conclusions can not be drawn, still it seems to be certain that the occurrence of ecdysteroids — just like in the families Caryophyllaceae and Chenopodiaceae — can only be characteristic of certain smaller taxonomic units within the families.

Discussion

Examinations of species belonging to various genera of the families Caryophyllaceae and Chenopodiaceae for ecdysteroid occurrence showed that these compounds could be detected in representatives of both families. There is similarity in the composition of ecdysteroids as well, namely, in each species found positive 20-hydroxyecdysone (β-ecdysone) was the main component. True, though, the occurrence of 20-hydroxyecdysone (β-ecdysone) is not restricted to the species of Centrospermae, as this compound is the main component in the ecdysteroid-containing species of Ranunculaceae, Compositae, Labiatae, etc., too, which are families taxonomically distant from the former ones. A more important difference is the occurrence of 2-deoxy-ecdysteroids beside the main component in many of the species examined from the family Caryophyllaceae, e.g. in *Silene*; these ecdysteroids have so far been isolated only from *Blechnum minus* so far, a species of Polypodiaceae. The detection of these derivatives in the family Caryophyllaceae is an important difference in comparison to the family Chenopodiaceae, particularly with other chemical characteristics, e.g. the presence or absence of betalaines; anthocyanins, pinits, etc. taken jointly into consideration.

The occurrence of ecdysteroids is not general either in Caryophyllaceae or in Chenopodiaceae, that is, its presence could not be pointed out for every species. The species *Silene*, *Lychnis* and *Melandrium* which belong to the Lychnideae tribe of the Silenoideae subfamily of the family Caryophyllaceae were found to be rich in ecdysteroids, while in genera belonging to other tribes ecdysteroids have not been detected so far. The restricted occurrence of ecdysteroids not only renders them suitable for taxonomic purposes, but in the concrete case of these genera it is also indicative of a close relationship between them. This supports those views of systematization in which *Silene* and *Melandrium* are regarded as one genus, as e.g. in the Flora Europea

(TUTIN 1964) where *Melandrium* as a separate genus does not exist. This contradicts, e.g. to Soó's opinion, who found the differentiation of the two genera reasonable (Soó 1970).

Similarly to the family Caryophyllaceae the family Chenopodiaceae is not generally characterized by the presence of ecdysteroids either. According to our investigations they are only characteristic of the representatives of the genera *Chenopodium*, *Spinacia*, *Atriplex*, *Beta* and *Kochia* of the subfamily Cyclolobeae.

We wish to emphasize that we regard our examinations as ones of preliminary character, so that more detailed examinations of further species are required to disclose deeper correlations, and only then will it be possible to draw a map of the ecdysteroid content, first of all within family.

REFERENCES

Abubakirov, N. K. 1981: Ekdisteroidy cvetkovih rastenij. *Khim. Prir. Soed.* **6:** 685–702.

Baltaev, U., Belov, M. N., Chumachenko, N. K., Abubakirov, N. K. 1984: High Performance Liquid Chromatography of Phytoecdysteroids of Melandrium Nutans *Khim. Prir. Soed.* **3:** 322–324.

Baltaev, U., Rashkes, Ya. V., Darmograi, V. N., Belov, Yu. P., Abubakirov, N. K. 1985: Phytoecdysteroids of Silene nutans. II. 22-Deoxyecdysterone and its Mass-spectra Characteristics. *Khim. Prir. Soed.* **1**: 62–66.

Baltaev, U., Rashkes, Ya. V., Abubakirov, N. K. 1986: Phytoecdysteroids of *Silene nutans* III. *Khim, Prir. Soed.* **4:** 522–525.

Báthori, M., Tóth, I., Szendrei, K., Minker, E., Blazsó, G. 1981: Ecdysteroids in Chenopodiaceae *Chenopodium album, Fitoterapia* **52:** 77–80.

Báthori, M., Tóth, I., Szendrei, K., Reisch, J. 1982: Ecdysteroids in *Spinacia oleracea* and *Chenopodium bonus-Henricus. Phytochemistry* **21:** 236–238.

Báthori, M., Tóth, I., Szendrei, K., Rattai, M., Minker, E., Blazsó, G. 1984: Ekdiszteroidok kimutatása és izolálása hazai libatopfélékből (Detection and isolation of ecdysteroids from Chenopodiaceae in Hungary). *Herba Hungarica*, **23:** 131–145.

Báthori, M., Szendrei, K., Herke, I., 1986: *Silene otites* (L.) Wib. ekdiszteroidjai [Ecdysteroids in *Silene otites* (L.) Wib.] *Herba Hungarica* **25:** 105–117.

Báthori, M., Szendrei, K., Herke, I. 1986a: Application of Combined Chromatographic Techniques in the Screening and Purification of Ecdysteroids. *Chromatographia* **21:** 234–238.

Báthori, M., Szendrei, K., Pelczer, I., Miklós, P. 1986b: Ecdysteroids of *Silene nutans* (L.) in: Kalász, H., Ettre, L. (Eds): *Chromatography* 85 Akadémiai Kiadó, Budapest.

Behnke, H. D., Turner, B. L., 1971: On specific sieve-tube *plastids in Caryophyllaceae. Taxon* **20:** 731–737.

Cronquist, R. K. 1986: *The Evolution and classification of Flowering Plants* Nelson, London and Edinburgh.

Dahlgren, R. D. 1977: Commentary on a Diagrammatic Presentation of the Angiosperms in Relation to the Distribution of Character States. *Plant Syst. Evol. Suppl.* **1:** 253–283.

Engler, A. 1964: *Syllabus der Pflanzenfamilien.* 12. Aufl. Grüber Bornträger, Berlin Nikolasse.

Grossheim, A. A., Schischkin, B. K. 1928: *Plantae Orientales Exiccatae.* Tiflis.

Hegnauer, R. 1964: *Chemotaxonomie der Pflanzen* III. Birkhäuser Verlag Basel u. Stuttgart.

Hutchinson, J. 1959: *Families of Flowering Plants.* Gawthorn, London.

Ikekawa, N. 1983: Sterol metabolism in insects and biosynthesis of ecdysone in the silkworm. *Experientia*, **39:** 466–473.

Mabry, T. J., Taylor, A., Turner, B. L. 1963: The betacyanins and their distribution. *Phytochemistry*, **2:** 61–64.

Maróy, P., Varga, J., Horváth, K. 1977: Rapid heterologous haptene radioimmunoassay for insect moulting hormone. *Febs. Letters*, **81:** 319–321.

Ohnishi, E., Takashi, M., Chatani, F., Ikekawa, N., Sakurai, S. 1977: 2-deoxyecdysone from Ovaries and Eggs of the Silkworm, *Bombyx mori. Science*, **197:** 66–67.

Ohnishi, E., Mizuno, T., Ikekawa, N., Ikeda, T. 1981: Accumulation of 2-deoxyecdysteroids in ovaries of the Silkworm, *Bombyx mori*. *Insect. Biochem.* **11:** 155–159.

Saatov, Z., Usmanov, B. Z., Abubakirov, N. K. 1979: Phytoecdysones of *Silene praemixta* I. Silenosterone. *Khim. Prir. Soed.*, **6:** 793–797.

Saatov, Z., Usmanov, B. Z., Abubakirov, N. K. 1979a: Phytoecdysones of *Silene praemixta* II. Praemixisterone. *Khim. Prir. Soed.*, **6:** 797–799.

Saatov, Z., Gorovits, M. B., Abdullaev, N. D., Usmanov, B. Z., Abubakirov, N. K. 1981: Sileneoside A — a new ecdysteroid-glycoside from *Silene brahuica* III. *Khim. Prir. Soed.* **6:** 738–644.

Saatov, Z., Gorovits, M. B., Abdullaev, N. D., Usmanov, B. Z., Abubakirov, N. K. 1982: Phytoecdysteroids of plants of Silene genus. IV. Sileneoside C—galactoside of integristerone A from *Silene brahuica*. *Khim. Prir. Soed.*, **2:** 211–214.

Saatov, Z., Gorovits, M. B., Abdullaev, N. D., Usmanov, B. Z., Abubakirov, N. K. 1982a: Phytoecdysteroids of Plants of Silene Genus V. Sileneoside B-digalactoside of ecdysterone from *Silene brahuica*. *Khim. Prir. Soed.*, **5:** 611–615.

Saatov, Z., Abdullaev, N. D., Gorovits, M. B., Abubakirov, N. K. 1984: Phytoecdysteroids of plants of Silene genus VI. 22-Sulphat-α-ecdysone — a novel ecdysteroide from *Silene brahuica*. *Khim. Prir. Soed.* **4:** 467–470.

Saatov, Z., Gorovits, M. B., Abdullaev, N. D., Usmanov, B. Z., Abubakirov, N. K. 1985: Phytoecdysteroids of the plants of Silene genus VIII. 2-Deoxyecdysterone-3-acetate from Silene praemixta. *Khim. Prir. Soed.*, **1:** 60–62.

Saatov, Z., Gorovits, M. B., Melibaev, S., Abubakirov, N. K. 1986: Phytoecdysteroids of Plants of Silene IX. Ecdysterone-22-0-Benzoat in Silene scabrifolia. *Khim. Prir. Soed.*, **1:** 77–80.

Saatov, Z., Abdullaev, N. D., Gorovits, M. B., Abubakirov, N. K. 1986: Phytoecdysteroids of Plants of Silene genus. X . Sileneoside E-2-deoxi-α-ecdisone-3-0-β-D-gycopyranoside- in *Silene bahurica*. *Khim. Prir. Soed.*, **3:** 323–326.

Soó, R. 1953: *Fejlődéstörténeti Növényrendszertan* (Phylogenetic System of Plants). Tankönyvkiadó, Budapest.

Soó, R. 1970: *A Magyar Flóra és Vegetáció Rendszertani, Növényföldrajzi Kézikönyve*. Vol. III. Synopsis Systematico- Geobotanicum Florae Vegetationisque Hungariae Tom. III. Akadémiai Kiadó, Budapest.

Takhtajan, A. 1973: Outline of the classification of flowering plants. *Botanical Review*. **46:** 226–359.

Tutin, T. G., Heywood, V. H., Burges, N. A., Valentine, D. H., Walters, S. M., Webb, D. A. 1964: *Flora Europaea*. Vol. I. Cambridge Univ. Press. 115–204.

Wettstein, R. 1935: *Handbuch der Systematischen Botanik* I–IV. Leipzig, Wien Fr. Deuticke.

Acta Botanica Hungarica 33 (3–4), pp. 387–393 (1987)

SCREENING FOR PLANT REGENERATION IN CALLUS AND PROTOPLAST CULTURES OF ALFALFA (*MEDICAGO SATIVA* L.) GERMPLASMS

LI SU NAM and HESZKY L. E.

DEPARTMENT OF GENETICS AND PLANT BREEDING, UNIVERSITY OF AGRICULTURAL SCIENCES, GÖDÖLLŐ, HUNGARY

(Received: 18 October, 1986)

Ovaries, hypocotyls and petioles of 21 germplasm-sources of *Medicago sativa* L. were used for callus induction and subsequent evaluation of plant regeneration. Most of the cultivars produced callus as much as 95% over the explants employed. Fifteen cultivars (71%) showed some degrees of plant regeneration. The results support the strong dependence of plant regeneration on genotype, explant and subculture. Cultivars with the highest frequency of regeneration were "Szentesi-délibáb" (46.7%) and "Rambler" (41.7%). The "Szentesi-délibáb" variety having shown a persistence in its regeneration capacity over three subcultures. Protoplasts isolated from Szentesi-délibáb and Szentesi-821 cultivars were cultured in a liquid medium. Plating efficiency was about 40–50%. Healthy plants were regenerated from the protoplasts of these two cultivars.

Introduction

Recovering plants from callus and protoplast is a crucial step, if widespread genetic manipulations are to be utilized in the breeding program. Regeneration of alfalfa (*Medicago sativa L.*) plants has been achieved from callus (SAUNDERS and BINGHAM 1972), suspension cultures (McCOY and BINGHAM 1977; NOVÁK and KONECNA, 1982) and protoplasts (KAO and MICHAYLUK, 1980; DOS SANTOS et al. 1980; LU et al. 1982).

MITTEN et al. (1984) reported a regeneration potential for 35 cultivars of a alfalfa germplasm source and showed intercultivar and intracultivar variations for regeneration capacities from callus cultures. ATANASSOV and BROWN (1984) also found genotypic dependence for regeneration capacity in protoplast-derived by callus of alfalfa.

BINGHAM et al. (1975) selected the alfalfa line "Regen S" to have a high frequency of regeneration by recurrent selection.

Screening and selection of a cultivar with good regeneration potential among commercial varieties, as well as further improvement of its' regeneration potential and application of a range of genetic manipulation could be necessary processes for alfalfa.

In this connection comparisons of regeneration potential in callus cultures and mesophyll protoplasts were carried out between 21 commercial cultivars of alfalfa, using the standard culture methods as described by SAUNDERS and BINGHAM (1972) and DOS SANTOS et al. (1980). The aim being to select cultivars with high regeneration potential in callus and protoplast cultures

Materials and methods

Donor plants: Seeds of 21 cultivars (Table 1) were provided by the Hungarian Gene Bank (Research Centre for Agrobotany, Tápiószele, Hungary).

Callus culture: Seeds were sterilized by the immersion in 0.2% (w/v) $HgCl_2$ for 10 mins followed by 4–5 rinses with sterile water and then were placed on hormon-free solid UM medium

Explants

Callus culture

Protoplast culture

Ovaries

Hypocotils, petioles

Leaves

Callus induction

Isolation of protoplast

BL 2Y

BL+2,4-D (2 mg/l)
+Kinetin (2 mg/l)
(30 days)

BL+2,4-D (20 mg/l)
+Kinetin (1 mg/l)
+Inositol (100 mg/l)
+YE (2 g/l)
(10 days)

KM 8p liquid culture
6,8 % glucose
2,4-D (0.2 mg/l)
NAA (1.0 mg/l)
Zeatin (0.5 mg/l)
(1 week)

Subculture on the same medium

Dilution 1-2 times with the same medium

BL+NAA (0.2 mg/l)
+Kinetin (2 mg/l)
+Inositol (100 mg/l)
+YE (2 g/l)
(20 days)

KM 8p-agarose embedded culture
(2 weeks)

Feeding with liquid KM 8p medium (3% glucose, 3% sucrose)
(2 weeks)

Hormone-free medium (BOi 2Y) for regeneration

Replacement of KM 8p medium with UM 6/0,6 (3% sucrose)
(1 week)

Transplantation of plantlets to greenhouse

Planting of colonies on UM 0.1/0.5
(4 weeks)

Fig. 1. **Protocol of culture procedures**

(Uchimiya and Murashige, 1974). *Petioles and hypocotyls* were excised from 2-week-old plants (15–20 plants per cultivars). The induction of embryogenesis and plant regeneration were followed by the Novák and Konecna (1982) methods (Fig. 1).

Floral buds with immature ovaries (1.5–2 mm in length) were collected from plants grown in the field and surface-sterilized with 96% alcohol for 1 min and then immersed in 5% (w/v) Neomagnol solution for 15 mins and rinsed with sterile water. *Immature ovaries* were isolated aseptically. Callus induction, embryogenesis and plant regeneration were carried out by using the method of Saunders and Bingham (1972). Basic medium was the modified Blaydes medium (BL) described in Saunders and Bingham (1972).

Protoplast culture. Three varieties (Szentesi-délibáb, Szentesi-821 and Rambler) exhibited the best regeneration capacity and were chosen as protoplast-donor plants.

Protoplasts were isolated from fully extended leaves of 3 to 4 week-old plantlets maintained aseptically in culture jars. The leaves were cut into 0.5–1 mm segments into a solution consisting of 0.375 M glucose and—200 mg/l $CaCl_2 \cdot 2H_2O$. When segmenting the leaves was completed the solution was removed and an enzymatic solution (Kao and Michayluk, 1980) diluted 1 : 1 with protopast culture medium (Kao and Michayluk, 1975) added. Enzymes used were desalted through Sephadex G-25 filtration. Overnight enzymatic digestion took place in the dark at a temperature of 25 °C. Protoplasts were released by gentle stirring, filtered through a sieve of a 70 μm pore size and washed twice with culture medium by centri-

fugation (100 g, 5 min). Protoplasts were cultured in plastic petri-dishes (5 cm) containing 3 ml of culture medium with a density of 2×10^5 protoplasts/ml. Dilution and gradual exchanges of medium were shown as indicated in Fig. 1.

Protoplast-derived calli were induced to embryogenesis in a UM 6/0.6 medium containing 6 mg/l 2,4-D (2,4-dichlorophenoxy acetic acid) and 0.6 mg/l kinetin. Regeneration of embryos and plants was established by transfering the calli to a hormone-free medium. Regenerated plants were grown to maturity in a greenhouse.

Results and discussion

I. Callus induction and plant regeneration

The data obtained by varying the types of explants of the 21 cultivars (Table 1) indicated that there were no significant differences between the cultivars in callus induction.

Most of the cultivars produced callus as much as 95% over the explants employed. The yellow, yellow-green and friably fast growing calli formed from the edges of each explant and the well developed calli gradually covered all the explants.

Ten days after inoculation 52% of the ovaries formed calli in the "Szarvasi" cultivar but only 6.5% in the "Nagyszénási". Such different responses during callus initiation may be due to the cultivars-specific requirements for nutrition and the phytohormones employed in the initial dedifferentiation process. Twenty days after culture initiation, the frequency of callus induction equalled the maximum in all cultivars tested.

Our major concern in the screening of cultivars was to compare the regeneration capacity in callus derived from the different explants of various germplasms using a standard sequence of media (Fig. 1). Regeneration capacity was estimated by the number of calli capable of regeneration in healthy plantlets, since many primitive structures of somatic embryos did not develop to cotyledonary embryos and plantlets. Calli cultured on the induction medium (ovary callus) and on the subculturing medium (hypocotyl and petiole callus) formed small spots and an intense green pigmentation. These green spots showed a rough surface under dissection microscopy. These structures were similar to semiorganized structures suggested by MITTEN et al. (1984). The occurrence of additional green spots not giving a conclusive indication of higher potentials in regeneration.

Callus originated from hypocotyl (Table 1) generally produced a higher ability for plant regeneration than that from ovary and petiole. Seventy-one percent (15 cultivars) of all varieties tested showed some degree of plant regeneration.

Cultivars with the highest percentage of regeneration were Szentesi-délibáb and Rambler (Table 1). Cultivars Nagyszénási, Iris, Saladina also showed better regeneration from a hypocotyl callus than that from the remain-

Table 1

Effect of genotype and explant on callus induction and plant regeneration in alfalfa (Medicago sativa L.)

Cultivars (origin)	Explant tissue	Callus induction %	Plant regeneration %
Kisvárdai-1 (Hungary)	Ovary	88.9	0
	Hypocotyl	100	20
	Petiole	100	10
Szentesi-délibáb (Hungary)	Ovary	95.3	12.5
	Hypocotyl	100	46.7
	Petiole	90.5	13.3
Szentesi-821 (Hungary)	Ovary	92.6	12.5
	Hypocotyl	100	13.3
	Petiole	100	0
Szarvasi (Hungary)	Ovary	96.0	0
	Hypocotyl	100	0
	Petiole	100	
7324/9 (Hungary)	Ovary	90.0	0
	Hypocotyl	100	0
	Petiole	100	
Vertivend (Hungary)	Ovary	88.9	0
	Hypocotyl	100	0
	Petiole	100	
Szarvasi-4 (Hungary)	Ovary	100	0
	Hypocotyl	100	12.8
	Petiole	100	
Tápiószelei (Hungary)	Ovary	100	0
	Hypocotyl	100	20
	Petiole	100	10
Nagyszénási (Hungary)	Ovary	100	0
	Hypocotyl	100	33.0
	Petiole	100	0
Iris (Denmark)	Hypocotyl	98.4	33.3
	Petiole	91.8	0
Orekeris (Netherland)	Hypocotyl	100	8.3
	Petiole	100	8.3
Alfa (Sweden)	Hypocotyl	98.5	0
	Petiole	98.5	8.3
Saladina (Argentina)	Hypocotyl	100	44.4
	Petiole	98.1	0
Morauska (Czechoslovakia)	Hypocotyl	100	0
	Petiole	97.9	0
Kayseri Jurecko (Turkey)	Hypocotyl	100	0
	Petiole	100	0
Pleven 1 (Bulgaria)	Hypocotyl	100	0
	Petiole	100	0
Malasria (Indonesia)	Hypocotyl	100	11.1
	Petiole	100	8.3
Heinrichs (Canada)	Hypocotyl	100	12.5
	Petiole	100	5.3
Kane (Canada)	Hypocotyl	100	14.3
	Petiole	100	0
Ramber (Canada)	Hypocotyl	100	41.7
	Petiole	100	41.7
Rangelander (Canada)	Hypocotyl	100	20
	Petiole	100	20

Table 2

Effect of subculture on plant regeneration from callus of different Hungarian cultivars and explants

Cultivars	Explants	Plant regeneration (%)		
		P_0	P_1	P_2
Kisvárdai-1	Ovary	0	0	0
	Hypocotyl	20.0	0	0
	Petiole	10.0	0	0
Szentesi-délibáb	Ovary	12.5	21.4	25.0
	Hypocotyl	46.7	33.3	0
	Petiole	13.3	0	0
Szentesi-821	Ovary	12.5	16.7	0
	Hypocotyl	13.3	0	0
	Petiole	0	0	0
Tápiószelei	Ovary	0	0	0
	Hypocotyl	20.0	0	0
	Petiole	10.0	0	0
Nagyszénási	Ovary	0	0	0
	Hypocotyl	33.0	0	0
	Petiole	0	0	0

P_0 = primary callus; P_1 and P_2 = first and second subculture of callus

der. These results indicate that Szentesi-délibáb and Rambler cultivars possess the highest percentage of genotypes capable to regenerate plants in callus cultures.

The callus of five cultivars (Table 2) was tested for regeneration capacity during subcultures. The results indicated that cultivar Szentesi-délibáb maintained plant regeneration over a longer duration than the others. Ovary callus showed a better persistance to regeneration whilst callus originated from petiole lost its' capacity after the first subculture.

II. Protoplast isolation and plant regeneration

From 21 cultivars screened, Szentesi-délibáb, Szentesi-821, and Rambler were chosen for the protoplast culture since their regeneration capacity was by for the best in callus culture.

Very healthy and stable protoplasts were isolated from the actively growing leaves of 3-week-old plants grown under aseptic conditions (Fig. 2). Initial culture protoplasts were aggregated in a liquid medium. The protoplast cultures then being diluted (about 30%) with fresh medium.

Protoplasts cultured in a Kao and Michayluk (1975) liquid medium KM8P containing 0.2 mg/l 2,4-D, 1.0 mg/l NAA (naphtylacetic acid) and 0.5 mg/l zeatin divided continuously and formed cell colonies (Fig. 2/b). Thirty-

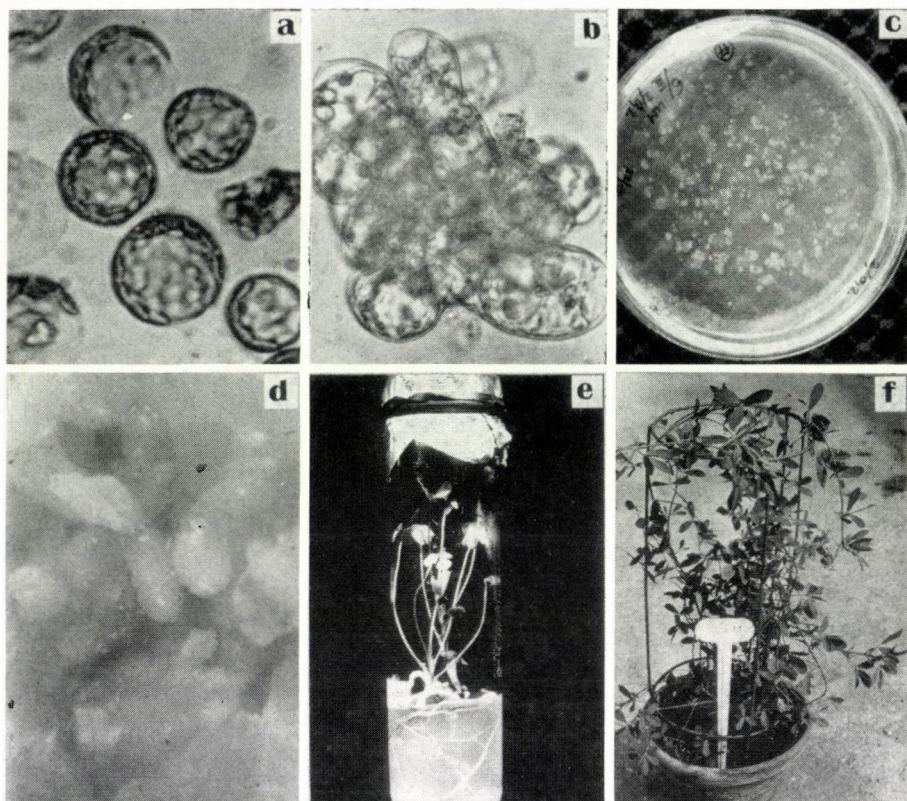



Fig. 2. Protoplast culture and plant regeneration in alfalfa (*Medicago sativa* L.) cultivar "Szentesi délibáb". — *a*: mesophyll protoplasts, *b–c*: formation of cell aggregates (*b*) and colonies (*c*) 10–30 days after isolation, *d*: somatic embryos developed in 70 day old culture, *e–f*: plant regeneration from somatic embryo

five days after the initiation of the culture, the cell colonies had reached 2–3 mm in size. Plating efficiency was about 40–50% in all three cultivars (Fig. 2/c).

To induce somatic embryogenesis, cell colonies were cultured in a UM 6/0.6 medium containing 6 mg/l 2,4-D and 0.6 mg/l kinetin for a week and then each individual colony was transfered to a solid-UM-medium supplemented with 0.1 mg/l 2,4-D and 0.5 mg/l kinetin. Calli of the three varieties grown in these media turned green and some green spots developed on the calli surface (Fig. 2/d).

Embryo germination and plant regeneration was established by transfering them a to BO/2Y medium. No embryo development succeeded in Rambler cultivar, however, 50 days after cultivation some embryos developed in the Szentesi-délibáb and Szentesi-821 cultivars. Plantlets were obtained in Szentesi-délibáb and Szentesi-821 cultivars seventy to eighty days after protoplast isolation. Plant development continued for about 2 months in this

medium. However, in some cases, abnormal plants were discovered. All the regenerated plants were grown in a greenhouse and seed set was normal (Fig. 2/f).

Our results support the strong dependence of plant regeneration on genotype, explant and subculture both in callus and protoplast cultures. There is also a possibility to isolate genotypes (e.g. Szentesi-délibáb, Szentesi-821) with capacities for high regeneration. Thus these two genotypes require further research in genetic manipulations.

ACKNOWLEDGEMENTS

We thank Dr. D. DUDITS and his co-workers for help with the preparation of protoplast, Dr. M. NAGY for supplying variety collection.

REFERENCES

Atanassov, A., Brown, D. C. W. 1984: Plant regeneration from suspension culture and mesophyll protoplasts of *Medicago sativa* L. *Plant Tissue Organ Culture*, **3:** 149–162.

Bingham, E. T., Hurley, L. V., Kaatz, D. M., Saunders, J. W. 1975: Breeding alfalfa which regenerates from callus tissue in culture. *Crop Sci* **15:** 719–721.

Dos Santos, A. V. P., Outka, D. E., Cocking, E. C., Davey, M. R. 1980: Organogenesis and somatic embryogenesis in tissue derived from leaf protoplasts and leaf explants of *Medicago sativa. Z. Pflanzenphysiol.*, **99:** 261–270.

Kao, K. N., Michayluk, M. R. 1975: Nutritional requirements for growth of Vicia hastaunana cells and protoplasts at very low population density in liquid media. *Planta*, **126:** 105–110.

Kao, K. N., Michayluk, M. R. 1980: Plant regeneration from mesophyll protoplasts of alfalfa. *Z. Pflanzenphysiol.*, **96:** 135–141.

Lu, D. Y., Pental, D., Cocking E. C., 1982: Plant regeneration from seedling cotyledon protoplasts. *Z. Pflanzenphysiol.*, **107:** 59–63.

McCoy, T. J., Bingham, E. T. 1977: Regeneration of diploid alfalfa plant from cells grown in suspension culture. *Plant Sci. Lett.*, **10:** 59–66.

Mitten, D. H., Sato, S. I., Skokut, T. A. 1984: In vitro regeneration potential of alfalfa germplasm sources. *Crop Sci.*, **24:** 943–945.

Novák, F. J., Konecna, D. 1982: Somatic embryogenesis in callus and cell suspension cultures of alfalfa (*Medicago sativa* L.) *Z. Pflanzenphysiol.*, **105:** 279–284.

Saunders, I. W., Bingham, E. T. 1972: Production of alfalfa plants from callus tissue. *Crop Sci.*, **12:** 804–808.

Uchimiya, H., Murashige, T. 1974: Evulation of parameters in the isolation of viable protoplasts from cultured tobacco cells. *Plant Physiol.* **54:** 936–944.

Acta Botanica Hungarica 33 (3–4), pp. 395–399 (1987)

INVESTIGATION OF THE INFLUENCE OF AZAAROMATICS ON THE CONTENTS OF ASSIMILATION PIGMENTS, SUGARS AND VITAMIN C IN THE CABBAGE AND LEEK

E. GURGUŁ, BARBARA HERMAN and WANDA ŚLIWA

INSTITUTE OF CHEMISTRY, PEDAGOGICAL UNIVERSITY CZĘSTOCHOWA, POLAND

(Received: 25. May 1987)

The influence of 1,5-, 1,6- and 4,6-benzo[h]naphthyridines on the contents of assimilation pigments, sugars and vitamin C was investigated in the cabbage and in the leek. The 1,5-benzo[h]naphthyridine was found to be the most active among three used azaaromatics.

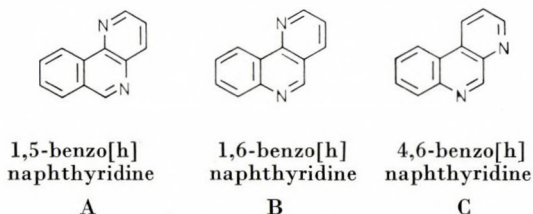
Introduction

For estimation of commercial value of vegetables, their appearance i.e. largeness, shape and colour, along with their flavour and taste are considered, while having in view their alimentary physiology the contents of organic and mineral substances in edible parts ought to be taken into account.

The internal quality of vegetables is due to the sum of various interacting factors; among them the most important are genetic processes, environment conditions and the kind of applied agrotechnics, e.g. used pesticides, growth regulators and fertilizers.

So far, an intensive research concerning factors influencing the scope of vegetables' harvest, as well as their alimentary value, i.e. the contents of mineral and organic compounds, along with some biologically active substances, is done (GURGUŁ 1982).

In the present work the influence of 1,5-, 1,6- and 4,6-benzo[h]naphthyridines (A–C, respectively) on the contents of assimilation pigments, sugars and vitamin C in cabbage and in leek has been investigated.

1,5-benzo[h] naphthyridine	1,6-benzo[h] naphthyridine	4,6-benzo[h] naphthyridine
A	B	C

Employed A–C are interesting from the biological point of view — these compounds as well as their derivatives exhibit a large antibacterial spectrum, and some of them have antineoplastic properties (ŚLIWA 1978).

Investigation of the activity of A–C against gram-positive and gram-negative bacteria has shown the rise of these activitities in the order B < C < A.

A–C have been found to increase the catalytic activity of peroxidase, catalase and acid phosphatase in cabbage and in leek (GURGUŁ *et al.* 1987).

Materials and methods

Experiments were carried out on vegetable cultures grown under a polyethylene foil. Plastic pots were filled up with brown soil, containing 1.7% of humus, the soil pH (KCl) being equal to 6.3.

At the start of experiments the contents of alimentary components was: 1.5 g N, 1.2 g K_2O, 0.8 g P_2O_5, 0.6 g MgO/pot. The ground moisture in all pots was kept on the equal level of 50% ppw of soil.

The influence of A–C, used at concentrations of 0.01 and 0.1% on the contents of assimilation pigments, sugars (in general) and vitamin C has been investigated in the white cabbage (*Brassica oleracea* var. *capitata* L.) from Enkhiuzen and in the leek (*Allium porrum*).

A–C have been synthesised in the Institute of Chemistry Pedagogical University in Częstochowa. The spray with A–C was made 15 days after seedling of cabbage and leek in pots, using ca 6 ml of aqueous solution of azaaromatic for each plant.

The plant material was investigated at the end of vegetation time, i.e. at the half of October. An average of measurements of 3 samples was taken, each sample providing from 20 cabbage outer leaves, or leek leaves, from 20 vertical pieces of cabbage heads and from 20 horizontal pieces from leek — roots, respectively.

The contens of pigments and vitamin C was determined in fresh plant material, and the contents of sugars (in general) in the plant material kept in the drier at 60–70 °C. The level of A and B chlorophylls was found with the BRUINSMA method (1963) and contents of sugars and vitamin C — with LUFF-SCHOORL and TILLMANS methods, respectively.

Results

The analytical data of the chlorophyll contents in leaves and in edible parts of cabbage and leek are summarized in Tables 1–3.

The average contents of the general chlorophyll in plants treated with A–C at concentrations of 0.01 and 0.1% was higher by 10.6–93.9% than that of control plants.

Table 1

Influence of 1,5-, 1,6-, and 4,6-benzo[h]naphthyridines on the contents of assimilation pigments in the edible parts of cabbage

		Chlorophyll contents in mg/dm³ of the fresh mass (%)								
		chlorophyll a			chlorophyll b			chlorophyll a+b		
Benzo[h] naphthy-ridine	Concentra-tion of aza-aromatic %	mg/dm³ of the fresh mass solution	%	differ-ence (%) as compa-with red control plant	mg/dm³ of the fresh mass solution	%	differ-ence (%) as compa-red with control plant	mg/dm³ of the fresh mass solution	%	differ-ence (%) as compa-red with control plant
Control		2.034	100	—	1.050	100	—	3.084	100	—
A	0.01	5.933	291.7	+191.7	2.732	260.2	+160.2	8.665	281.0	+181.0
B		2.276	111.9	+ 11.9	1.047	99.7	— 0.3	3.322	107.7	+ 7.7
C		4.904	241.1	+141.1	2.182	207.8	+107.8	7.086	229.8	+129.8
$\frac{A+B+C}{3}$		4.371	214.9	+114.9	1.987	189.2	+ 89.2	6.358	206.2	+106.2
A	0.1	5.088	250.1	+150.1	2.168	206.5	+106.5	7.257	235.3	+135.3
B		1.394	68.5	— 31.5	0.798	76.0	— 24.0	2.192	71.7	— 28.9
C		2.637	129.6	+ 29.6	1.323	126.0	+ 26.0	3.961	128.4	+ 28.4
$\frac{A+B+C}{3}$		3.040	149.5	+ 49.5	1.430	136.2	+ 36.2	4.470	145.0	+ 45.0

Table 2

Influence of 1,5-, 1,6-, and 4,6-benzo[h]naphthyridines on the contents of assimilation pigments in outer leaves on cabbage

		Chlorophyll contents in mg/dm³ of the fresh mass (%)								
		chlorophyll a			chlorophyll b			chlorophyll a+b		
Benzo[h] naphthyridine	Concentration of azaaromatic (%)	mg/dm³ of the fresh mass solution	%	difference (%) as compared with control plant	mg/dm³ of the fresh mass solution	%	difference (%) as compared with sontrol plant	mg/dm³ of the fresh mass solution	%	difference (%) as compared with control plant
Control		5.787	100	—	1.910	100	—	7.697	100	—
A	0.01	8.643	149.3	+49.3	3.952	206.9	+106.9	12.595	163.6	+63.3
B		4.979	86.0	−14.0	1.552	81.2	− 18.8	6.531	84.8	−15.2
C		6.992	120.8	+20.8	2.504	131.1	+ 31.1	9.496	123.4	+23.4
$\frac{A+B+C}{3}$		6.871	118.7	+18.7	2.669	139.7	+ 39.7	9.541	124.0	+24.0
A	0.1	7.855	135.7	+35.7	3.170	166.0	+66.0	11.025	143.2	+43.2
B		2.964	51.2	−48.8	1.640	85.9	−14.1	4.604	59.8	−41.2
C		7.546	130.4	+30.4	2.956	154.8	+54.8	10.502	136.4	+36.4
$\frac{A+B+C}{3}$		6.122	105.8	+ 5.8	2.589	135.5	+35.5	8.710	113.2	+13.2

Table 3

Influence of 1,5-, 1,6- and 4,6-benzo[h]naphthyridines on the contents of assimilation pigments in the leaves of leek

		Chlorophyll contents in mg/dm³ of the fresh mass (%)								
		chlorophyll a			chlorophyll b			chlorophyll a+b		
Benzo[h] naphthyridine	Concentration of azaaromatic (%)	mg/dm³ of the fresh mass solution	%	difference (%) as compared with control plant	mg/dm³ of the fresh mass solution	%	difference (%) as compared with control plant	mg/dm³ of the fresh mass solution	%	difference (%) as compared with control plant
Control		11.926	100	—	5.989	100	—	17.915	100	—
A	0.01	17.133	143.7	+43.7	9.209	153.8	+53.8	26.342	147.0	+47.0
B		14.217	119.2	+19.2	6.127	102.3	+ 2.3	20.344	113.6	+13.6
C		14.263	119.6	+19.6	6.767	113.0	+13.0	21.030	117.4	+17.4
$\frac{A+B+C}{3}$		15.204	127.5	+27.5	7.368	123.0	+23.0	22.572	126.0	+26.0
A	0.1	15.390	129.0	+29.0	8.54	142.6	+42.6	23.93	133.6	+33.6
B		7.886	66.1	−33.9	4.199	70.1	−29.9	12.086	67.5	−32.5
C		14.463	121.3	+21.3	7.131	119.1	+19.1	21.594	120.5	+20.5
$\frac{A+B+C}{3}$		12.580	105.5	+ 5.5	6.623	110.6	+10.6	19.203	107.2	+ 7.2

A and B irrespectively on their concentration have been found to stimulate at the highest degree the level of general chlorophyll in both kinds of vegetables.

In rosetta — leaves as well as in heads of cabbage, the treatment of A at the concentration of 0.01% increased the level of the general chlorophyll by 63.6–181%, and in leek leaves by 47%, while in the case of 0.1% concentration this growth was 43.2–135.3% for cabbage and 33.6% for leek

The use of C at the 0.01% concentration caused in the same parts of plants the increase of chlorophyll contents by 23.4–129.8% for cabbage and 17.4% for leek, while at the 0.1% concentration the increase of chlorophyll contents was only 28.4–36.4% in cabbage and 20.5% in leek (Tables 1–3).

Table 4

Influence of 1,5-, 1,6- and 4,6-benzo[h]naphthyridines on the contents of sugars (in general) in the cabbage and in the leek

Benzo[h]naphthyridine	Concentration of azaaromatic (%)	Sugar contents (mg %)	
		in the cabbage	in the leek
Control	—	3.0	4.2
A	0.01	4.5	6.0
B		3.7	4.8
C		4.2	5 1
(A+B+C)/3		4.1	5.3
A	0.1	5.5	5.8
B		4.9	5.0
C		5.0	5.3
(A+B+C)/3		5.1	5.4

Table 5

Influence of 1,5-, 1,6- and 4,6-benzo[h]haphthyridines on the vitamin C contents in the cabbage and in the leek

Benzo[h]naphthyridine	Concentration of azaaromatic (%)	Vitamin C contents (mg %)	
		in the cabbage	in the leek
Control	—	49.4	38.2
A	0.01	61.6	57.3
B		40.4	30.0
C		54.6	30.0
(A+B+C)/3		52.2	39.1
A	0.1	68.2	29.3
B		60.3	24.5
C		64.1	27.2
(A+B+C)/3		64.2	27.1

In the case of B the negative influence on the chlorophyll level was found (Tables 1–3).

In our experiments the considerable influence of A–C on the contents of sugars was observed so in the cabbage as in the leek (Table 4). The average increase of the sugars' level was 37% in cabbage and 26% in leek at concentrations of 0.01%, at concentrations of 0.1% this increase being 70% in cabbage and 30% in leek. The highest rise of the whole contents of sugars was found for A and C.

Investigated A–C showed a positive influence on the vitamin C level in cabbage at both concentrations, while in the case of the leek the increase of the vitamin C contents was observed only for A at the concentrations of 0.01% (Table 5). Thus, in both processes — syntheses of assimilation pigments and of vitamin C, the highest biological activity was found for A and C.

The 1,6-isomer also in this case showed the lowest biological activity.

Discussion

Among three benzo[h]naphthyridines A–C, used in the above experiments, A and C showed the highest biological activity; they influence considerably the nutritive value of edible parts of cabbage and leek, measured by the contents of assimilation pigments, sugars (in general) and vitamin C at the harvest time.

Obtained results are in accordance with our experiments concerning the influence of A–C on the catalytic activity of peroxidase, catalase and acid phosphatase in cabbage and in leek (GURGUL *et al.* 1987). So far the results of the present work allow to consider A and C as substances of a high biological activity, exhibiting a positive influence so on the quality of plants, as well as on the scope of their harvest.

REFERENCES

Bruinsma, J. 1963: Investigation of the chlorophyll contents in the leaves extracts, *Photochem. and Photobiol.*, **2:** 241.

Gurguł, E. 1982: Wpływ nawadniania oraz nawożenia azotem i magnezem na aktywność niektórych enzymów, plonowanie oraz skład chemiczny kapusty głowiastej czerwonej i włoskiej, Rozprawy AR Szczecin, 84.

Gurguł, E., Śliwa, W., Herman, B. 1987: The influence of benzo[h]naphthyridines on the catalytic activity of peroxidase, catalase and acid phosphatase in cabbage and leek at their development process, *Biochemie und Physiologie der Pflanzen* (in press).

Śliwa, W. 1978: Badania nad benzo[h]naftyrydynami, Prace Nauk. Instyt. *Chemii org. i Fiz. Politechniki Wrocł., Ser. Studia i Materiały*, 13/8, Wrocław.

Acta Botanica Hungarica 33 (3—4), pp. 401—405 (1987)

INVESTIGATIONS INTO THE CAUSES OF STERILITY II. *TABEBUIA PENTAPHYLLA* L.

R. KUMAR* and GARGI SINGH

DEPARTMENT OF BOTANY, R. B. S. COLLEGE, AGRA, INDIA
DEPARTMENT OF BOTANY, AGRA COLLEGE, AGRA-282 002, INDIA

(Received: 15 November 1986)

The effects of the malfunctioning tapetum on the deposition and degradation of callose wall around microspore tetrads in *Tabebuia pentaphylla* L. were studied. In 60% of the microsporangia the secretary tapetum starts disintegrating at the microspore tetrade stage. In such anthers the tetrads are well developed and show a prominent callose wall around them. Such anthers produce fertile pollen grains. On the other hand, in remaining 40% microsporangia tapetum shows abnormal behaviour and consequently becomes hypertrophied. The microspore tetrads in such anthers are devoid of callose wall and shrivel. A higher callose activity of hypertrophied tapetum is responsible for premature degradation of callose resulting in the production of sterile and non-viable pollen grains.

Introduction

The "special mother cell wall" of BEER (1911) which is primarily made up of callose, is deposited within the original cellulose wall as the PMC'S advance into the prophase of meiosis. A number of workers suggested a multitude of essentional functions of both the callose deposition and its degradation during microsporogenesis (see VASIL 1967). According to ESCHRICH (1962), HESLOP-HARRISON (1964) and FRANKEL *et al.* (1969), the deposition of callose in the PMC'S at early prophase is essential for the onset of synchronous meiotic division in the anthers.

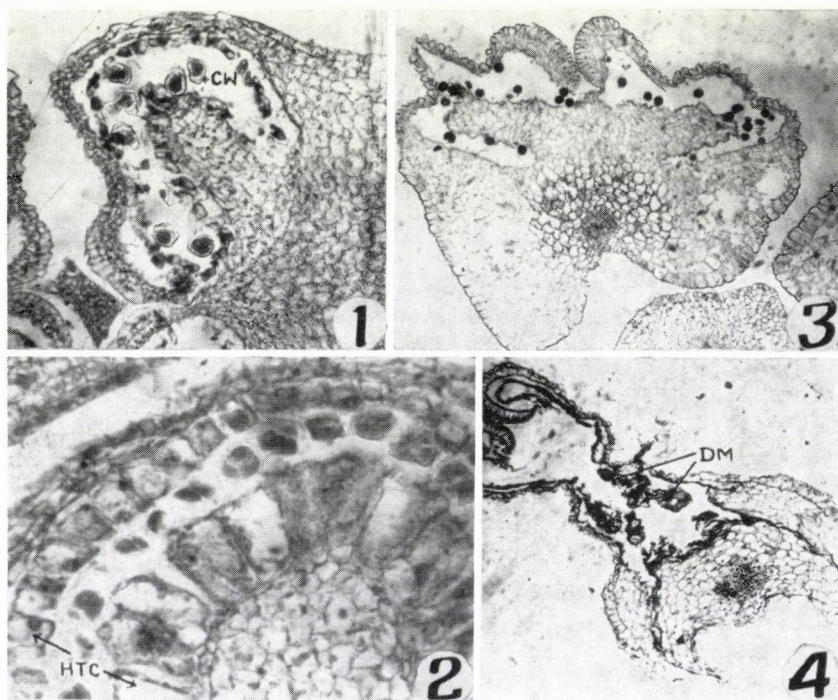
As the microspores released from the special callose wall, both the callose and pectic compounds of the cell plate are hydrolysed rapidly. The soluble products resulting from such hydrolysis are then available for metabolism by the microspores and are also a possible substrate source for the development of pollen exine and for pollen nutrition (LARSON and LEWIS 1962; ESCHRICH 1964; WATERKEYN 1964; IZHAR and FRANKEL 1971). Available information except of FRANKEL *et al.* (1969) and GUPTA and NANDA (1974) on callose deposition degradation and its function during microsprogenesis in sterile anthers is scanty. The present study had been undertaken to gain precise information concerning the role of the tapetum on pollen development in *Tabebuia pentaphylla* a plant which does not set seed under the environmental conditions of Agra.

* Present adress: Central Sericultural Research and Training Institute, Srirampuram, MYSORE-570 008. India.

Materials and methods

Buds and flowers of *Tabebuia pentaphylla* L. were collected from the horticultural garden, Agra and were fixed in CARNOY's for one hour and finally stored in 70% ethanol. The usual methods of dehydration and embedding were followed for investigating the ontogeny and development of the tapetum. The sections were cut at 6–15 micron thickness and stained with HEIDENHAIN's iron–alum haemotoxylin. For localizing total insoluble polysaccharides, periodic acid SCHIFF's (PAS) reaction was used (JENSEN 1962, see Table 1). The callose was detected by the method of CHEADLE *et al.* (1953).

Observations

During the course of investigation on the anther development in *Tabebuia* we came across to an interesting phenomenon. In 60% of the microsporangia the pollen mother cells (PMC) follow the normal pattern of growth resulting in the formation of fertile pollen grains with dense cytoplasm (Fig. 3). In such anthers the tapetum starts disintegrating at microspore

Figs 1–2. T. S. of anthers of *Tabebuia pentaphylla* L. at tetrad stage stained with Heidenhains iron-alum haematoxylin

Figs. 3–4. T. S. anthers stained with PAS reaction

Fig. 1. Normal anthers, disintegrating tapetal cells and the tetrade having callose walls (CW). ×210

Fig. 2. Sterile anther, tapetal cells are hypertrophied (HTC) and tetrads are lacking in callose wall ×280

Fig. 3. Fertile anther with viable pollen grains containing reserves ×180

Fig. 4. Sterile anther note the degenerated mass of pollen (DM) ×180

mother cell tetrad stage and at the time of microspore formation the tapetal cells are seen as a degenerated narrow line on the inner side of anther cavity (Fig. 1). In remaining 40% of the microsporangia where the tapetum does not follow the usual mode of development, its cells become hypertophied containing dense cytoplasm. In such anthers the pollen grains remain non-viable and formed a degenerated mass of pollens (Figs 2, 3, 4).

The callose wall in fertile anthers start depositing between the plasmalema and the primary wall of the PMC'S early in the meiotic prophase, usually in late leptotene. The deposition is first seen in corners of cells within the original mother cell wall. The accumulation of callose continues during the entire period of meiosis and reaching its peak at the tetrad stage. As callose deposition takes place around the PMC'S it extends as thin bands in between the microspores as well and forms a continuous band around the tetrads (Fig. 1). Now the four microspores of a tetrad are released by the break-down of the callose wall enclosing them. Later on no trace of callose is available. In anthers where the tapetum is abnormal and showing the hypertrophy the microspore tetrads show a different mode of development. In these anthers, most of tetrads do not show any callose wall, while a few have only a fragmentary of it (Fig. 2). On the basis of the present studies it appears that the extent of hypertrophy of tapetal cells is inversely proportional to the amount of traceable callose present around tetrads. It is also noticeable here that in microsporangia with hypertrophied tapetum the callose can disappear in early stages as well when it can be already detectable in other normal anthers where the tapetum does not show any abnormalities. Thus, it is clear from the present investigation that the behaviour of the tapetum influences not only the pollen fertility and development of fibrous thickening in endothecium (KUMAR 1979), but also callose deposition and its degradation around developing microspore tetrads.

Discussion

In normal anthers the callose starts accumulating prior to the onset of meiosis in the PMC'S (BEER 1911; ESCHRICH 1964; HESLOP-HARRISON 1964; CHRISTENSEN 1972; KUMAR 1979). In the opinion of the present authors the lack of the callose in sterile microsporangia of *Tabebuia* in comparison to fertile ones in all probability due to the rapid degradation by enzymes, subsequently the normal callose wall is not retained in spite of its synthesis at early stage. MEPHAM and LANE (1969) detected a demonstrable callose present in tapetal cytoplasm, responsible for the break-up of tetrads in *Tradescantia bracteata*. Our assumption get support from the present studies as callose wall development has been observed at young stages where the tapetum does not show any hypertrophy. On the other hand, where the anther deviates from its normal course of development and tapetum showed hypertrophy in such cases it seems that the synthesized callose is hydrolysed due to the exces sive callase produced by the hypertrophied tapetum as compared to the fertile anthers (tapetum does not show any hypertrophy) where well defined callose wall persist much longer. Our observations lend support to the findings of FRANKEL *et al.* (1969) and GUPTA and NANDA (1974) in sterile microsporangia of *Petunia* and *Allium*, respectively. According to their school of thought the callose is hydrolysed under the influence of excessive production of enzyme

Table 1

Total carbohydrates of insoluble polysaccharides-PAS reaction

Species investigated	Control	PAS Reaction	
		Oxidation in 0.5% Periodic acid	Schiff's reagent at room temperature (32 °C)
Tabebuia pentaphylla	Acetylation 6 hrs at 58–60 °C	20 minutes	15 minutes

callase by hypertrophied tapetum. Thus, it can be coined as the premature degradation of callose which is essential foı the programmed control of meiosis and normal development of young microspores (HESLOP-HARRISON 1964) is no longer available. Further, it is also clear from the present studies that the quantity and the time of degradation of callose are important factors in the normal development of the PMC'S and its activity, too, is different for fertile and sterile microsporangia (see FRANKEL *et al.* 1969).

So far, persistence, delayed degeneration or hypertrophy of the tapetum have been associated with the production of non-viable pollen grains (SINGH 1965; KAUL 1970; KINOSHITA 1971; CHAUHAN and KINOSHITA 1980a). According to these studies the transfer of the nutrients to the developing microspore is blocked by the hypertrophied tapetum. So, in want of food material they become vacuolate and sterile. Present studies further strengthen the role of tapetum in pollen development. However, further studies are needed to understand exact role of tapetum in governing the behaviour and activity of callose in fertile and sterile microsporangia.

ACKNOWLEDGEMENTS

The authors are thankful to Dr. S. V. S. CHAUHAN for guidance and to the Council of Scientific and Industrial Research, New Delhi, for the financial assistance.

REFERENCES

Beer, R. 1911: Studies in the spore development. *Ann. Bot.* **25:** 199–214.

Chauhan, S. V. S., T. Kinoshita, 1980a: Morphological and histochemical studies on pollen degeneration in cytoplasmic male-sterile sugar beet (*Beta vulgaris* L. var. *saccharifera*) *J. Fac. Agric. Hokkaido Univ.* **56:** 435–451.

Cheadle, V. I., E. M. Gifford, K. Esau. 1953: A staining combination for phenol and contiguous tissues. *Stain, Technol.* **28:** 49–53.

Christensen, J. E., H. T. Horner, Jr., N. R. Lersten 1972: Pollen wall and tapetal orbicular wall development in *Sorghum bicolor* (Graminae). *Amer. J. Bot.* **59:** 43–58.

Eschrich, W. 1962: Elektronenmikroskopische Untersuchungen an Pollen Mutterzellen-callose IV. Mitteilung uber callose. *Protoplasma* **55:** 419–422.

Eschrich, W. 1964: Die callose Synthese bei Pollen Mutterzellen von *Cucurbita ficifolia.* In H. F. Linskens: ed. "*Pollen Physiology and Fertilization*" North Holland Publ. Co., Amsterdam. pp. 48–51.

Frankel, R., S. Izhar, J. Nitsan 1969: Timing of callose activity and cytoplasmic male sterility in *Petunia. Biochem Genet.* **3:** 451–455.

Gupta, S. C., K. Nanda 1974: Malfunctioning tapetum and callose wall behaviour in *Allium cepa.* microsporangia. *Beitr. Biol. Pflanzen.* **50:** 465–472.

Heslop-Harrison, J. 1964: Cell wall, cell membrane and protoplasmic connectionsduring meiosis and pollen development. In H. F. Linskens ed. "*Pollen Physiology and Fertilization*" North Holland Publ. Co., Amsterdam. pp. 39–47.

Izhar, S., R. Frankel, 1971: Mechanism of male sterility in *Petunia*: The relationship between pH, callose activity in the anthers and the breakdown of the microsporogenesis. *Theor. Appl. Genet.* **41:** 104–108.

Jensen, W. A. 1962: *Botanical Histochemistry.* W. H. Freeman and Co., San Francisco and London.

Kaul, C. L. 1970: Investigations into the causes of sterility, II. *Tabernaemontana coronaria* Willd. *Cytologia,* **35:** 570–576.

Kinoshita, T. 1971: Genetical studies on the male sterility of sugar beets (*Beta vulgaris* L.) and its related species. *J. Fac. Agric. Hokaido Univ.* **56:** 445–541.

Kumar, R. 1979: Investigations into the causes of fruitlessness and seedlessness in *Tecoma stans* and *Tabebuia pentaphylla* L. Ph. D. Thesis, Agra University, Agra.

Larson, D. A., C. W. Lewis, Jr. 1962: Pollen wall development in *Parkinsonia aculeata. Grana Palynol.* **3:** 21–27.

Mepham, R. H., G. R. Lane. 1969: Formation and development of the tapetal periplasmodium in *Tradescantia bracteata. Protoplasma,* **68:** 175–192.

Singh, S. P. 1965: Role of tapetum in pollen development. *Palynol. Bull.* **1:** 11–14.

Vasil, I. K. 1967: Physiology and cytology of anther development. *Biol. Rev.* **42:** 327–373.

Waterkeyn, L. 1964: Callose of the microsporocyte and the pollen In: H. F. Linskens ed. "Pollen physiology and fertilization" pp. 52–58.

Acta Botanica Hungarica 33 (3—4), pp. 407—411 (1987)

EFFECT OF NEW SYNTHETIC REGULATORS ON BIOMASS AND ALKALOID PRODUCTION BY CALLUS TISSUES OF *LOBELIA INFLATA* L.

Krajewska, A.,[1] Szőke, É.,[1] Botz, L.,[2] Szarvas, T.[3]

[1] SEMMELWEIS MEDICAL UNIVERSITY, INSTITUTE OF PHARMACOGNOSY H-1085 BUDAPEST, ÜLLŐI ÚT 26.

[2] HUNGARIAN ACADEMY OF SCIENCES, ECOLOGICAL AND BOTANICAL RESEARCH INSTITUTE, H-2163 VÁCRÁTÓT

[3] HUNGARIAN ACADEMY OF SCIENCES, ISOTOPE INSTITUTE, H-1525 BUDAPEST, PF. 77.

(Received: 12 December 1986)

The authors produced callus tissues of leaf origin from *Lobelia inflata* and studied in various combinations the effect of new synthetic cytokinin-like regulators and alkaloid precursor amino acids on the biomass- and alkaloid production of the tissues, with special regard to lobeline, an alkaloid of pharmacological importance. They found that phenylalanine added to the culture medium besides 1 mg/l Sz/28 was optimum for the growth and lobeline content of the tissues. The total alkaloid content, on the other hand, was highest in response to Sz/11 (1 mg/l) plus phenylalanine.

Introduction

The tissue culture methods offer wide possibilities for following the action of synthetic growth regulators, e.g. yield-increasing substances, herbicides. In the case of medicinal plants it is particularly important to study the formation of therapeutically active secondary plant products in addition to the biomass production.

In the course of our work we tried to find out how the new cytokinin-like growth regulators (1,4-dihydroxy-phthalazine biguanidine salt marked Sz/11 and N-isopropyl-benzimidazol chloride marked Sz/28) would act on the biomass- and alkaloid production of *Lobelia inflata* callus tissues, with special regard to the pharmacologically active lobeline.

The effects of the growth regulators Sz/11 and Sz/28 were earlier studied in callus tissues of *Datura innoxia* Mill. The Sz/28 increased the biomass production of the cultures by 30 and their alkaloid production by 60 per cent. Besides, it greatly promoted the incorporation of radioactive phenylalanine (a precursor of tropan-skeleton alkaloids) into the tropan alkaloids first — of all into hyoscyamine — whereby the total alkaloid content was further increased (Szőke et al. 1984).

The herb of *Lobelia inflata* contains more than 20 piperidine base alkaloids. Its main alkaloid is L-lobeline ((—)cis-8,10-diphenyl-lobelionol) though lobelanine, nor-lobelanine, lobelanidine, etc. occur in considerable quantities in it (Hegnauer 1966). Lobeline is mainly used as an analeptic in the case of poisoning by gas and narcotics, but *Lobelia* alkaloids are also used in therapy as components of preparations against asthma and smoking (additive effect to that of nicotine).

Wysokinska (1977) was the only author who produced *Lobelia* tissue cultures. She raised the callus tissue induced from the growing tip of shoot on Schenk—Hildebrandt (1972) culture medium. The callus tissues showed the highest rate of growth under the influence of 10^{-6} M 2,4-D, but the alkaloid production was better promoted by 10^{-5} M IES or 10^{-7} M NES.

Table 1

Effects of regulators and amino acid precursors on the growth, alkaloid- and

Culture medium	Concentration of regulators mg/l				Amino acids M/l	
	2,4-D	Kinetin	Sz/11	Sz/28	Phe	Lys
AMS-2	1	1	—	—	—	—
S	—	—	—	—	—	—
Kin-1	—	1	—	—	—	—
Sz/11–1	—	—	1	—	—	—
Sz/28–1	—	—	—	1	—	—
2,4-D+Sz/11+Phe	1	—	1	—	10^{-4}	—
2,4-D+Sz/11+Lys	1	—	1	—	—	10^{-4}
2,4-D+Sz/28+Phe	1	—	—	1	10^{-4}	—
2,4-D+Sz/28+Lys	1	—	—	1	—	10^{-4}

Material and method

The callus tissues induced from the leaves of sterile seedlings were raised on Murashige—Skoog (1962) culture medium of mineral- and vitamin composition in dark (2500 lux). The regulators were added to the culture medium in various concentrations (1, 10, 50 mg/l), the alkaloid precursor amino acids (phenylalanine, lysine) in a quantity of 10^{-4} M.

The growth data of the callus tissues were determined after Szőke et al. (1979). The total alkaloid content in the cultures was determined photometrically (Mahmoud—El-Masry 1980), while for the lobeline content thin layer chromatography was followed by a densitometric determination at 249 nm (typ.: CS 920 SHIMADZU HIGH SPEED TLC SCANNER).

The selective analytical VRK separation of the alkaloids of *Lobelia* tissue cultures was carries out by the application of the recently elaborated so-called PRIZMA-model (Nyiredy 1985, Krajewska et al. 1986).

Layer: Kieselgel 60 F_{254} Merck DC-alufolien Solvent system: tetrahydrofurane ((1,1): acetone (1,1): diethylamine (2,8): hexane (15,0).

Results and evaluation

From callus tissues of leaf origin of *Lobelia inflata* kept on a Murashige—Skoog culture medium of mineral- and vitamin composition containing 1 mg/l kinetin and 1 mg/l 2,4-D (AMS-2) a vigorously growing tissue line could be produced after some one and a half year. The growth of the cultures reached 95 mg daily, and they retained their capacity for alkaloid biosynthesis (Table 1).

When the cultures were kept on hormone-free culture medium (S) their growth intensity considerably decreased, which suggests that they are hardly — if at all — capable of endogenous hormone synthesis.

When new type regulators were added to the culture medium instead of the conventionally used growth regulating substances, the growth indices and alkaloid production of the cultures changed. The Sz/11 regulator adding at a concentration of 1 mg/l considerably increased the growth of the cultures compared to the S culture medium, while at higher concentrations (10 and 50 mg/l) it caused significant growth inhibition (Table 1 and Fig. 1). On the other hand, in cultures showing the lowest rate of growth (50 mg/l Sz/11) the alkaloid content (%) was higher than in the vigorously growing ones containing 1 mg/l Sz/11, or in

lobeline content and alkaloid production of Lobelia inflata callus tissues

Fresh weight, g		Dry matter content %	Increase value		Growth rate (mg/day)	Total alkaloid content %	Alkaloid production mg/culture	Lobeline content %
$\bar{x}$	$S_{\bar{x}}$		by fresh weight	by dry weight				
7.780	0.169	4.45	5.84	5.97	94.90	0.003	0.010	0.002
1.859	0.127	8.41	0.64	2.14	10.32	0.002	0.003	0.002
1.887	0.135	4.64	0.66	0.76	10.72	0.001	0.001	0.001
4.084	0.467	4.95	2.59	3.06	42.05	0.004	0.008	0.002
4.650	0.143	7.14	3.09	5.68	50.19	0.007	0.022	0.002
6.298	0.306	4.06	4.54	4.14	73.73	0.015	0.038	0.004
6.524	0.574	4.26	4.74	4.59	76.96	0.010	0.028	0.004
7.234	0.395	3.69	5.36	4.37	87.10	0.008	0.021	0.006
6.406	0.485	4.90	4.64	5.32	75.28	0.008	0.025	0.005

those raised either on S or AMS-2 culture medium. However, as regards the alkaloid production (per dry weight of 1 culture) the callus tissues kept on a culture medium containing 1 mg/l Sz/11 are considered better (Table 1).

The regulator *Sz/28* also stimulated the growth of the callus tissue, though an increase in its concentration — similarly to Sz/11 — resulted in significant growth inhibition. The daily growth of the cultures was reduced almost to half (Fig. 2).

An analysis of the percentage total alkaloid content of the cultures reveals that in response to 1 mg/l Sz/28 it increased compared to both callus tissues grown on S- or AMS-2 basic culture media and those kept on culture media containing 1 mg/l kinetin or Sz/11 (Table 1).

In order to increase more the alkaloid production of the cultures phenylalanine and lysine were added to the culture medium, considering that they are the precursor amino acids of the piperidine base alkaloids that characterize the genus *Lobelia* (DONOVAN 1975).

However, the callus tissues grown on the basic culture medium containing 1 mg/l kinetin and 1 mg/l 2,4-D responded with a significantly reduced growth and alkaloid production to either lysine or phenylalanine (Fig. 3).

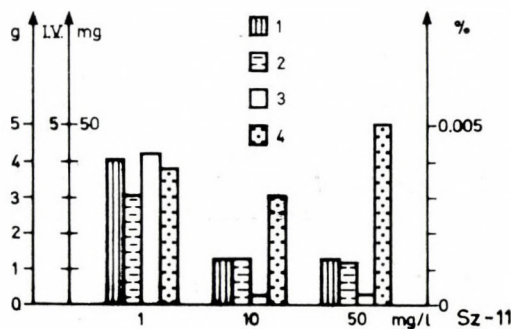



Fig. 1. Effect of Sz/11 on the growth and alkaloid content of *Lobelia inflata* callus tissue — 1. Fresh weight (g) — 2. Increase value on dry weight basis — 3. Daily growth (mg) — 4. Alkaloid content (%)

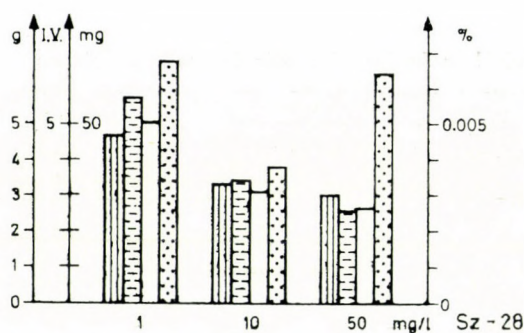



Fig. 2. Effect of Sz/28 on the growth and alkaloid content of *Lobelia inflata* callus tissue. (See Fig. 1.)

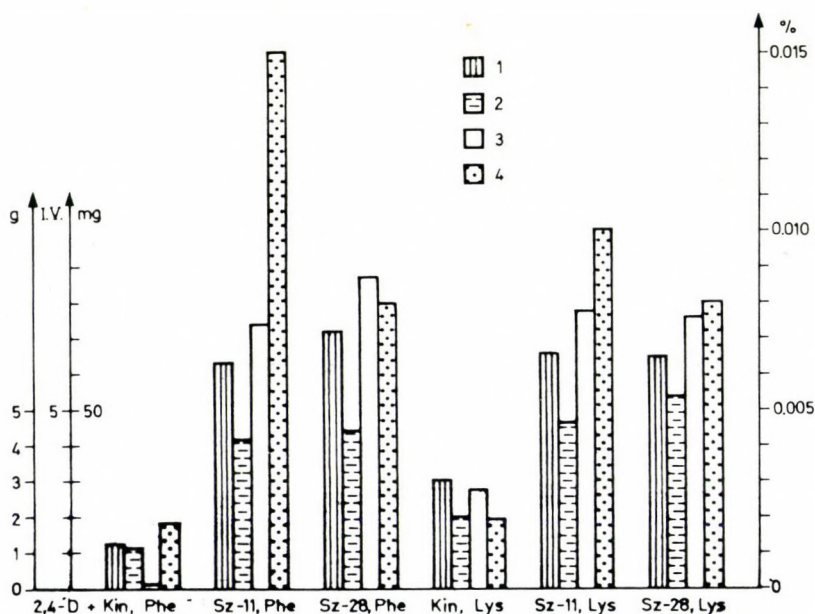



Fig. 3. Effects of regulators and precursor amino acids on the growth and alkaloid content of *Lobelia inflata* callus tissue. (To the culture medium 1 mg/l 2,4-D, 1 mg/l cytokinin-like regulator and 10^{-4}M amino acid were added.) (See Fig. 1)

Considering that in *Datura innoxia* callus tissues the Sz/28 promoted the incorporation of phenylalanine into the alkaloids (SZŐKE *et al.* 1974) we tried to add new synthetic regulators instead of kinetin to the culture medium in the presence of the precursor amino acids in the case of the *Lobelia* callus, too.

1 mg/l Sz/11 combined with either phenylalanine or lysine greatly stimulated the growth of the callus tissues compared to the kinetin, and at the same time considerably increased the alkaloid content (Fig. 3). In combination with phenylalanine it increased fivefold while with lysine threefold the percentage total alkaloid content in the cultures. Since the tissues grw well, these culture medium combinations can be considered very good from the point of view

of alkaloid production (mg/culture) as well (Table 1). The formation of lobeline is also outstandingly good in callus tissues grown on culture media of this type (Table 1).

With Sz/28 (1 mg/l) added to the culture medium containing phenylalanine the growth of the tissues was even more intensive (significant) than under the influence of Sz/11, but the total alkaloid content was raised to a lesser extent (Fig. 3). From the point of view of lobeline biosynthesis, on the other hand, the action of Sz/28 is highly favourable; the highest lobeline content is found in callus tissues grown on a culture medium containing phenylalanine, too (Table 1).

Summary

It can be established that in callus tissues of leaf origin from *Lobelia inflata* the biomass-, alkaloid- and lobeline production will be equally optimum if the new synthetic regulators (Sz/11 and Sz/28) are applied in combination with alkaloid precursor amino acids (phenylalanine, lysine).

REFERENCES

Donovan, D. G., Long, D. J., Forde E., Geary, P. 1975: The biosynthesis of *Lobelia* alkaloids. Part III. Intermediates in the biosynthesis of 8, 10-diethyl-lobelidione. *J. Chem. Soc. Perkin Trans I*, **5:** 415–419.

Hegnauer, R. 1966: *Chemotaxonomie der Pflanzen.* Bd. 4. Birkhauser Verlag, Basel und Stuttgart, pp. 404–414.

Krajewska, A., Szőke, É., Petri, G., Botz, L., Szarvas, T. 1986: Új szintetikus regulátorok hatása a *Lobelia inflata* L. organizáltatott kultúrák alkaloidképzésére (Effect of new synthetic regulators on the alkaloid production of organized cultures of *Lobelia inflata* L.). *XXIV. Vándorgyűlés, Gödöllő.*

Mahmoud, Z. F., El-Masry, S. 1980: Colorimetric determination of lobeline and total alkaloids in *Lobelia* and its preparations. *Sci. Pharm.*, **48:** 365–368.

Murashige, T., Skoog, F. 1962: A revised medium for rapid growths and bioassays with tobacco tissue cultures. *Physiol. Plant.*, **15:** 473–497.

Nyiredy, S., Erdelmeier, C. A. J., Meier, B., Sticker, O. (1985): „Prisma": Ein Modell zur Optimierung der mobilen Phase für die Dünnschichtchromatographie, vergestellt anhand verschiedener Naturstofftrennungen. *Planta Med.*, 51: 241–246.

Pozsár, B., Szarvas, T., Maróti, M. 1980: Effect of the cytokinin-like regulators (Sz)11 and Sz(28) on the stimulation of the mitose frequency, the protein synthesis, the photosynthetic $^{14}COf_2$ fixation and the HTO photolysis by the leaves of pinto bean. *Bot. Közlem.*, **67:** 313–314.

Schenk, R. V., Hildebrandt, A. C. 1972: Medium and techniques for induction and growth of monocotyledonous and dicotyledonous plant cell cultures. *Can. J. Botany*, **50:** 199–204.

Szőke, É., Kuzovkina, I. N., Verzár-Petri, G., Szmirnov, A. M. 1979: Növekedést befolyásoló anyagok hatása a kamilla (*Matricaria camomilla* L.) kallusztenyészetek biomasszaképzésére (Effect of growth regulating substances on the biomass production of callus cultures of chamomile (*Matricaria camomilla* L.). *Herba Hung.*, **18:** 41–57.

Szőke, É., Szarvas, T., Pozsár, B. J., Verzár-Petri, G. 1984: Effect of a new synthetic cytokinin-like regulator on the tissue culture, and alkaloid production of *Datura innoxia*, *Acta Biochem. Biophys. Acad. Sci. Hung.*, **19:** 62.

Wysokinska, H. 1977: Wystepowanie alkaloidow w hodowli tkankowej *L. inflata* L. *Farm. Pol.* **33:** 725–727.

Acta Botanica Hungarica 33 (3—4), pp. 413—420 (1987)

MORPHOLOGY AND GERMINATION CHARACTERISTICS OF *ARISTIDA SETACEA* SEEDS

S. K. PATTNAIK and M. K. MISRA

DEPARTMENT OF BOTANY BERHAMPUR UNIVERSITY, BERHAMPUR 760007 ORISSA, INDIA

(Received: 10 April 1987)

Aristida setacea a native tufted perennial grass occurs in gravelled and sandy habitats with extreme moisture conditions. The seed output and reproductive capacity of the plant is very high. The average weight on the seed is 1.103 mg. Acid treatment and scraping revealed seed coat dormancy in the species. Percentage germination was more in diffuse light compared to dark and continuous light. Optimum temperature for highest germination rate was 30 °C. Effect of different wavelengths of light on germination was not remarkable. Low hydrogen ion concentration (acidic range) favoured the germination of *Aristida setacea* compared to higher concentration (alkaline range). The germination percent maxima was observed in pH 3.

Introduction

Aristida setacea Retz. a native tufted perennial semiarid grass grows in extreme moisture conditions in gravelled rocky uplands as well as in sandy soils. It attains a highest of *Ca* 1.5 m. Apart from its economic use as broom and green fodder in helps for soil conservation. No information is available on the morphology of seed and germination behaviour of this plant. Germination regulation play an important role in ecology of plants, persistence of weeds and in relation to plant breeding (TOOLE *et al.*, 1956). When the response of seeds to various environmental conditions such as light, temperature, pH, chemicals, etc. is analysed it shows the nature of different blocks in seed dormancy indicating the physiological processes involved. Much work has been done on the seed morphology, output and ecophysiology of seed germination in a number of temperate and tropical species. Seed coat and embryo dormancy in particular in several species has been studied by DATTA and SEN (1982); BASKIN and BASKIN (1969); MISRA (1963); BOOJH and RAMAKRISHNAN (1982); TANWAR and SEN (1980); BHATIA and SEN (1978) and CHATTERJI and SEN (1964). SALISBURY (1942) stated that the difference in size and shape of the seeds help in more efficient segregation in their dispersal.

The objective of this present investigations was to study the seed output pattern and its morphology along with the seed germination characteristics.

Materials and Methods

1. Seed output and morphology

Aristida setacea occupies an important position in the grasslands of the Berhampur University campus especially in the uplands and hillocks. Four lots each of one hundred plants were collected during November and December 1984. Number of tillers per plant (tuft), inflorescences per tiller and seeds per inflorescence were counted randomly. The total number of

seeds per plant were then calculated. Total length of ovary and awn was considered as the length of the seed. The average length and weight of a seed expressed taking 100 seeds into consideration. Reproductive capacity through seeds was studied from the germination behaviour of the collected seeds according to SALISBURY (1942).

2. Germination Study

Few hundred healthy and matured seeds were collected and perfectly air dried to avoid fungal infection and stored in air-tight bottles under normal laboratory conditions. For germination, moist chambers were prepared in petriplates with sterilised cotton covered by sterilised Whatman No. 1 filters papers being soaked with distilled water. Intact seeds did not germinate revealing seed coat dormancy. Seeds were scarified by removing a portion of seed coat (scraping) with the help of a needle without damaging the embryo or endosperm or by treating the seeds with concentrated sulphuric acid (36 N) for different time periods ranging from 15 to 60 seconds. Immediately after the acid treatment the seeds were washed thoroughly in tap and distilled water; then used for germination studies. As the optimum time period for acid treatment to the seeds to break seed coat was 30 seconds, this time period was fixed for acid treatment to break the seed coat, after which the effect of light, temperature, and pH on germination was studied. The germination experiments were performed within two months of collection. Petriplates alongwith Whatman No. 1 filter papers at the bottom were used for germination studies in all experiments and test solutions or distilled water was added to the petriplates as and when required. Four replicates were taken for each observation for each treatment. Germination was observed on the seventh day and the experiment was performed in normal room temperature. The results so obtained were subjected to statistical analyses.

3. Light

Growth chambers with three 40 Watt fluorescent tubes were used to study the effect of wavelengths on seed germination. Celophane papers and thick black papers were covered in petriplates to generate wavelenghts (colours) and complete darkness, respectively. A control set was observed simultaneously.

4. Temperature

For germination at different temperatures petriplates were placed inside the BOD incubator, maintained constantly at the desired temperature.

5. pH

Solutions of different hydrogen ion concentrations were prepared by adding either hydrochloric acid or sodium hydroxide to distilled water being measured accurately with the help of a digital pH meter. The pH levels of the solutions used were 2.0 to 12.0.

Results

1. *Seed output*

Observation on average number of tillers, seeds per tiller and seeds as a whole per plant revealed that these parameters were comparatively less in grazed open area than the protected area, with a difference of about 5 tillers, 100 seeds/tiller and 1500 to 1600 seeds/plant (Table 1). Seed output in this plant was very high compared to many dicot and monocot plants. The reproductive capacity through seeds in grazed and open area were 2793 & 3935 respectively (Table 1).

2. *Size and weight of seeds*

Appreciable difference was not found in size and weight of seeds collected from grazed and protected areas. Average lengths of ovule, awn and seed were 12.0 ± 0.4, 26.6 ± 1.1 and 38.6 ± 1.4 mm, respectively, and weight of 100 seeds was 110.3 ± 9.1 mg (Table 1).

3. *Seed Germination*

Effect of scarification and acid treatment

When the seeds were treated with sulphuric acid at time periods ranging from 15 to 60 seconds, the rate of germination responded between 10 to 93% (Table 2). However, from this result it was revealed that acid treatment to seeds for 30 seconds was the optimum time period to breek the seed coat dormancy. The maximum rate of germination observed in this treatment was 93 per cent. Similar observation was also resulted when the seeds were germinated after scraping the seed-coat.

4. *Effect of Light*

Diffused light responded high rate of germination (75%) followed by complete dark (60%) and continuous light (40%) (Table 3). The effect of different colour of light (wave-length) on germination of seeds showed little difference. However, the difference in seed germination under red and yellow light was noticeable (Table 3).

Table 1

Seed output, size and weight of seeds and reproductive capacity of Aristida setacea plant (Average ± S.E.M)

Site of collection	No. of tillers/tuft.	No. of seeds/tiller	No. of seeds/tuft	Length of ovary mm	Length of awn mm	Total length of seed mm	Seed weight mg/seed	Reproductive capacity
Protected	18±2	247±27	4240 ±476	12.0 ±0.4	26.6 ±1.1	38.6 ±1.4	1.10 ±0.09	3935
Grazed	14±1	194±20	3003 ±223	10.5 ±0.3	23.2 ±0.8	33.7 ±1.1	0.95 ±0.08	2792

Table 2

Effect of scarification on germination of seeds of Aristida setacea

	Concentrated Sulphuric Acid treated in seconds						Scraped without acid treatment
	15	20	30	40	50	60	
Percentage of germination (± S.E.M.)	21±3	63±3	93±5	85±3	60±3	10±5	93±5

Table 3

Effect of light, dark and colour (wave length) treatment on germination of A. setacea seeds

	Nature of Light			Wavelength of light			
	Complete dark	Diffused light	Continuous light	Red	Yellow	Green	Blue
Percentage of germination (± S.E.M.)	60±4	75±11	40±10	38±5	25±12	35±6	37±7

Table 4

Effect of temperature on the germination of Aristida setacea seeds

	Temperature °C in BOD incubator						
	15	20	25	30	35	40	45
Percentage of germination (± S.E.M.)	0	13±3	40±8	73±8	55±8	50±7	0

5. *Effect of Temperature*

Table 4 reveals the effect of various temperature regimes on the seed germination of *A. setacea*. The optimum temperature for highest percent of germination (73%) was 30 °C and the values decreased both in decreasing or increasing temperatures. At the two extreme temperatures, that is at 15 °C and 45 °C, no seeds of the species germinated. Difference in small range of temperature (5 °C) showed a wide gap in percent germination from the maximum value (Table 4). The results also revealed that decreased temperatures were more detrimental to the process than the increased temperatures.

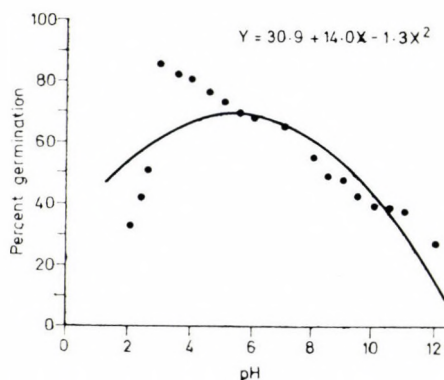



Fig. 1. Relationship between pH and percent germination for *Aristida setacea*

6. *Effect of pH*

Figure 1 revealed that with increase in pH the percent of germination increased upto pH 3 which was found to be the most suitable point where the percent of germination was highest (85%). Beyond pH 3 the percent of germination decreased gradually and it was more remarkable in alkaline range. There was no germination in pH 13. This indicated that higher pH (alkaline) ranges were more detrimental than the acid range.

Discussion

Aristida setacea possess a quality of producing large quantities of seeds for increasing their population to a greater extent as in case of other grasses and herbs. Reduction in the number of seeds and reproductve capacity in open field was due to the removal of vegetative parts through grazing. Similar findings were reported by AMBASHT and MAURYA (1970) for *Dichanthium annulatum*. Lower seed output accompanied by reduction in the percentage germination resulted in a further fall in the reproductive capacity in relation to grazing which was in uniformity with the reports of SANT (1963 and 1963a).

Seed coat scarification of *A. setacea* seeds increased the germination rate without any loss of viability indicating the presence of seed coat dormancy. TOOLE *et al.* (1956), MALL (1957), KAUL (1959) and SINGH (1965) had reported improved germination by decoating the seed coat in different species. THURSTON (1960) and HARPER (1957) had reported that dormant weed seeds which possess hard and thick seed coat are valuable and ecologically significant features for their survival.

Destruction of seed coat by the action of concentrated sulphuric acid on *A. setacea* seeds increased the germination rate is in conformity with the findings of DATTA and SEN (1981) in some leguminous seeds through the action of sulphuric acid. Degradation of components of the seed coat by the chemical action of the acid is analogous to the deterioration caused by microbes in soil. Seed coat of *Aristida setacea* were made permeable in nature by microbial activity. It is often stated that hard seed coat is an inherited feature, being determined in some cases by environmental effects on the mother plant. DATTA and SEN (1981a) reports that environment profoundly influences the germination response in two ways, conditions existing during seed formation as well as location of seed on the mother plant. According to LEOPOLD and KRIEDEMANN (1975), higher temperatures usually enhance that state of dormancy rather than improving the germination process. According to RAMAKRISHNAN and KHOSLA (1971), the seed coat (husk) dormancy of *Digitaria* and *Echinochloa* was due in part to the presence of a water soluble inhibitor only during the first months after harvest.

Light intensity had little effect on germination of *A. setacea* seeds. Maximum percent of germination in diffused light (Table 3) indicates less

light requirement supporting the views of BAKSHI and KAPIL (1952), JOSHI *et al.* (1967) and KOLLER (1957). KUMAR *et al.* (1971) reported that germination in cases of *Cenchrus trifolorus* and *Dactyloctenium aegyptium* was inhibited by light. PANDEY (1969) stated that light period of 12 hrs or more caused more or less inhibitory effects in *Anagallis arvensis*. The effect of colour of light (wavelength) in the present study was not remarkable. However, higher percentage in red light followed by blue light confirms the findings of NEGBI and KOLLER (1964) and SANTRA *et al.* (1981). Stimulatory effect of red light may be explained by considering the photo conversion of the phytochrome Pfr in which it evidently initiates a chain of processes that ultimately results in germination. AGARWAL and PRAKASH (1978) had stated that the seed germination was promoted by high energy region of the visible spectrum (blue light). ISIKAWA (1957) observed stimulation of germination of *Nigella* by long irradiation with blue light which confirms our findings.

Maximum germination was obtained at 30 °C correlating the environmental conditions of the region. The average atmospheric temperatures of the region is well within the range (daily maximum varied from 27.2 to 32.6 °C). This further confirms the reports of BABU and JOSHI (1970) in *Borreria articularis* which showed germination maxima at 35 °C and KYMAR *et al.* (1971) reported maximum germination in *Dactyloctenium aegyptium* and *Cenchrus biflorus* at 30 °C and 35 °C, respectively. However, maximum germination was reported at 15 °C for *Schima khasiana* and at 20–25 °C for *S. wallichii* by BOOJH and RAMAKRISHNAN (1982). Low germination rate in higher temperatures in our findings was probably due to the deletorious effect of temperature on the physical state of the cellular component. No germination of *A. setacea* seeds at 45 °C showed loss of viability and permeability. DATTA and SEN (1983) showed that at lower temperature (20 °C) both inhibition and germination improved with the progress of storage in *Desmodium gangeticum* seeds.

Percent of germination in seeds of *A. setacea* with respect to different ranges of pH revealed a curvilinear relationship (Convex hyperbola) (Fig. 1). The better germination in the acid range over alkaline range may be due to the favourable nature of the seed to the enzymatic process involved during the seed germination. Further it was observed by MISRA (1978) that the plant generally grows on acidic soils. For the prediction of percentage of germination (dependent variable) at any particular pH (independent variable) a quadratic secondary degree regression of orthogonal polynomial type was fitted to the data.

$$Y = a + b\,x + c\,x^2$$

where Y and x represents the percentage of germination and pH, respectively. The correlation coefficient ($r = -0.539$) was found to be significant at 5%

level. Our findings relating to the effect of pH on germination is in conformity with the findings of SINGH *et al.* (1975) on four grass seeds.

ACKNOWLEDGEMENTS

We are thankful to Prof. B. N. MISRA, Head, Department of Botany, Berhampur University for facilities.

REFERENCES

Agarwal, P. K., Prakash, G. 1978: Control on seed germination in some Indian trees. *Trop. Ecol.* **19:** 174–177.

Ambasht, R. S., Maurya, A. M. 1970: Reproductive capacity of *Dichnthium annulatum* Stapf. in relation to biotic factors. *Trop. Ecol.* **10:** 186–193.

Babu, V. R., Joshi, M. C. 1970: Studies on physiological ecology of *Borreria articularis* (Linn. f) F. N. Will. — A common weed of bajra (*Pennisetum typhoides* (Burm. F.) Staf. et. C. E. Hubb.) fields. *Trop. Ecol.* **11:** 126–139.

Bakshi, T. S., Kapil, R. N. 1952: The autecology of *Mollugo nudicaulis* Lam. *Bull. Bot. Soc. Bengal.* **6:** 45–48.

Baskin, C. C., Baskin, J. M. 1969: Germination and dormancy in cedar glade plants. IV. *Isanthus brachiatus, Panicum capillare, Cyperus inflexus, Eragrostis spectabilis* and *Ruellia humilis. J. Tennessee Acad. Sci.* **44:** 69–70.

Baskin, J. M., Baskin, C. C. 1974: Breaking dormancy in seeds of *Isanthus brachiatus* (Labiatae) with gibberellic acid. *Fyton, Gaspar Campos.* **861:** 159–165.

Bhatia, P. R., Sen, D. N. 1978: Adaptive polymorphism in *Ipomea pes-tigridis* (Convolvulaceae), a common rainy season weed of the Indian arid zone. *Plant Syst. & Evol.* **129:** 111–117.

Boojh, R., Ramakrishnan, P. S. 1982: Seed germination and seedling establishment of the two closely related *Schima* species. *Proc. Ind. Acad. Sci.* **91:** 397

Chatterji, U. N., Sen, D. N. 1964: On the ecophysiology of *Salmalia malabarica* (DC.) Scho. & Endl. seeds. *Sci and Cult.* **30:** 598–600.

Datta, S. C., Sen, S. 1981: Germination study on seven legumes and non-legumes. *Bot. Közlem.* **68:** 285–288.

Datta, S. C., Sen, S. 1981a: Effect of the environment of the mother plants of *Cassia sophera* var. *purpurea* on the germination of their seeds. *Acta Bot. Acad. Sci. Hung.* **27:** 319–323.

Datta, S. C., Sen, S. 1982: Environment-controlled seed dormancy in *Cassia sophera* var. *purpurea. Geobios.* **9:** 86–88.

Datta, S. C., Sen, S. 1983: Thermo control of seed germination in *Desmodium gangeticum. Proc. Nat. Acad. Sci. India.* **53:** 11–18.

Harper, J. L. 1957: The ecological significance of dormancy and its importance in weed control. *Proc. 4th Internat. Cong. Crop Protection,* Hamburg. 415–420.

Isikawa, S. 1957: Interaction of temperature and light in the germination of *Nigella* seeds. I., II. *Bot. Mag. (Tokyo)* **70:** 264–275.

Joshi, M. C., Kahate, S. and Bishnoi, S. 1967: Autecology studies on Rajasthan desert plants. II. *Tribulus terrestris. Linn. J. Indian Bot. Soc* **46:** 169–184.

Kaul, V. 1959: Distribution of *Xanthium strumarium* L. complex in India. *Proc. 46th Indian Sci. Congr. Part IV*: 8–9.

Koller, D. 1957: Germination regulating mechanisms in some desert seeds. IV. *Atriplex dimorphostegia* Kar. et. Kir. *Ecology.* **38:** 1–13.

Kumar, A., Joshi, M. C., Babu, V. R. 1971: Some factors influencing the germination of seeds in two desert grasses. *Trop. Ecol.* **12:** 202–208.

Leopold, A. C., Kriedemann, P. E. 1975: *Plant Growth and Development.* Tata McGraw-Hill, New Delhi.

Mall, L. P. 1957: Contribution to the autecology of *Cassia tora* L. and *C. obtusifolia* L. *Bull. Bot. Soc. Univ. Saugar.* **7:** 14–21.

Misra, B. N. 1963: Germination of seeds of *Ipomoea crassicaulis* (Benth.) Robinson. *J. Indian Bot. Soc.* **42:** 358–366.

Misra, M. K. 1978: Phytosociology and primary production of a grassland community at Berhampur, Orissa (India). Ph. D. Thesis, Berhampur Univ., Berhampur, India.

Negbi, M., Koller, D. 1964: Dual action of white light in the photocontrol of germination of *Oryzopsis miliacea*. *Plant Physiol.* **39:** 247–253.
Pandey, S. B. 1969: Photo control of seed germination in *Anagallis arvensis* L. *Trop. Ecol.* **10**: 96–138.
Ramakrishnan, P. S., Khosla, A. K. 1971: Seed dormancy in *Digitaria adscendens* (H. B. K.) Henr. and *Echinochloa colona* Link. with particular reference to covering structures. *Trop. Ecol.* **12:** 112–122.
Salisbury, E. J. 1942: *The Reproductive Capacity of Plants.* G. Bell and sons Ltd., London.
Sant, H. R. 1963: Effect of grazing on the general herbage of Banaras Hindu University ground and a study of seed and reproductive capacity of four weeds. *Proc. Nat. Acad. Sci. India.* **33:** 355–360.
Sant, H. R. 1963a: Ecological studies in *Dichanthium annulatum* Stapf. with special reference to reproductive capacity in relation to grazing. *Proc. Nat. Inst. Sci. India 30B:* 354–372.
Santra, S. C., Adheya, T. K., Desarkar, D. K. 1981: Ecological studies on *Bidens pilosa* L.: Effect of light, temperature, salt and different extracts on seed germination and seedling growth. *Trop. Ecol.* **22**(2): 162–169.
Singh, J. S. 1965: Influence of scarification on germination of *Cassia tora* L. seeds. Rept., 480/Ecol. Project, B.H.U., Varanasi-5, India.
Singh, V. P., Mall, S. L., Billore, S. K. 1975: Effect of pH on germination of four common grass species of Ujjain (India). *J. Range Manage.* **28:** 497–498.
Tanwar, G. S., Sen, D. N. 1980: Germination behaviour in dimorphic seeds of *Melothria maderaspatana* L. *Flora.* **170:** 351–353.
Thurston, J. M. 1960: Dormancy in seeds. In: *The Biology of Weeds.* (Symp. of British Ecol. Soc.) Ed. J. L. Harper, Blackwell Scientific Pub. Co. Ltd., Oxford.
Toole, H. H., Hendricks, S. B., Borthwick, H. A., Toole, V. K. 1956: Physiology of seed germination. *Ann. Rev. Plant Physiol.* **7:** 299–324.

Acta Botanica Hungarica 33 (3–4), pp. 421–430 (1987)

DISTRIBUTION OF PHOTOSYNTHATES IN THE LEAVES OF TWO MAIZE LINES IN THE INITIAL PHASE OF THE PHOTOPERIOD

TÉCSI L., MARGÓCZI K., MARÓTI I.

JÓZSEF ATTILA UNIVERSITY, DEPARTMENT OF BOTANY, RESEARCH GROUP OF THE HUNGARIAN ACADEMY OF SCIENCES, SZEGED, P.O. Box 657

(Received: 10 December 1986)

Malate-, starch-, sucrose- and monosaccharide contents were studied in detached leaves of the Pioneer 165 and F2 inbred maize lines in the first hour of light following a 8-hour dark period.

The plants were grown in phytotron under two different photon flux densities (200 μmol · m^{-2} · s^{-1} and 100 μmol · m^{-2} · s^{-1}) for 40 days.

The genotype dependence of the levels of the above-mentioned metabolites, and their temporal changes at various photon flux densities were studied.

The malate level increased, the monosaccharide- and starch levels decreased, while the sucrose level hardly changed at lower photon flux density.

The malate-, monosaccharide- and starch levels of the leaves began to rise slowly after a temporary decrease, while the sucrose level showed a significant increase even in the first minutes of light.

The leaves of the genotype Pioneer 165 were characterized by higher malate and monosaccharide contents compared to genotype F2.

The genotype Pioneer 165 was more sensitive to reduction of the photon flux density, which manifested in decrease of dry weight and increase of water content.

The temporal changes of the examined metabolites show that the genetic factors exercise a greater influence on the photosynthetic induction period than the environmental factors, such as photon flux density.

Introduction

At the beginning of the photoperiod, when photosynthesis starts, considerable changes take place in the photosynthetizing tissues. To expose the biochemical bases of these changes extensive investigations are carried on.

Some of the photosynthetic enzymes (NADP-ME, PPDK, F1,6BPE) are known to be light controlled in vivo: in the induction period, when the leaves were illuminated after a dark treatment, their enzymes reached maximum activity level in 2.5 minutes (USUDA *et al.* 1984).

The regulating enzymes, metabolites of the carbohydrate metabolism play an important role during the induction period. They mostly influence the distribution of carbon fixed in the starch and sucrose (FONDY and GEIGER 1985, HUBER *et al.* 1984, SHARKEY *et al.* 1985). Such regulating mechanisms are: (1) the regulation of the SPS enzyme (SICHER and KREMER 1985), (2) the molecula of F2,6BP regulating the general decomposition-reconstruction of sugar in the plant cytoplasm (SMYTH and BLACK 1984, PAZ *et al.* 1985), (3) the regulatory protein required for the activation of PPDK (BAER and SCHRADER 1985), (4) the role of aspartate in the transportation of PGA, DHAP and malate (BOAG and JENKINS 1985), (5) the regulation of ADPG-pyrophosphorylase (PREISS 1982).

It is also important to expose the relation between the biochemical metabolism and the productive capacity of the plant. In this field investigations were made by SUGIYAMA *et al* (1984) who found that the levels of the PEPC and PPDK enzymes in the maize were in much closer relation with the biomass than the RuBisCO level under optimum conditions of growth; the reduction of light intensity caused first of all an increase in the quantity of PEPC and PPDK, while the ratio of RuBisCO decreased.

In isolated maize bundle sheath chloroplasts neither the malete decarboxylation nor the CO_2 assimilation was found to be without the other activity suggesting a very close correlation between these processes; NADPH required for the carbon reduction cycle mostly can be replaced in the course of the decarboxylation of malate by NADP-ME (JENKINS and BOAG 1985).

We measured in our experiments the quantity of non-structural carbohydrates and malate in mature leaves of the P165 and F2 inbred maize lines in the first hour of the photoperiod. According to the preliminary examinations in the first minutes of illumination the O_2 production is quicker, while the non-photochemical extinction of the chlorophyll-a fluorescence and the deepoxidation of the violaxanthin are slower in the P165 leaf than in that of the F2 genotype; the average number of thylakoid/granum in the mesophyll chloroplasts is higher in the P165 than in the F2 genotype (PATAKY and MARÓTI 1985, MARÓTI 1986).

On the basis of the results evaluation of the influence of various light intensities and genotypes was made on the photosynthetic induction and on the distribution and accumulation of carbohydrates and malate respectively.

Material and method

1. Plant cultivation

Pioneer 165 and F2 lines of maize (*Zea mays* L.) were grown in phytotron (HORVÁTH 1972) water content up to the age of 40 days, in a mixture of sand and perlite (1 : 1) the of which was kept at 70 % of water capacity. The plants were grown at two light intensities: 200 μmol · m^{-2} · s^{-1} and 100 μmol · m^{-2} · s^{-1} (Tungsram F33 fluorescent tube), in a 16–8-hour light-dark period.

The 600 cm^3 culture pots contained 3 plants in each were given 20 cm^3 nutrient solution twice a week. The macroelements of the nutrient solution were: K^+ (4mM), Na^+(1 mM), Ca^{2+} (5 mM), Mg^{2+} (12 mM), Cl^- (1 mM), NO_3^- (12 mM), SO_4^{2-} (1,2 mM), $H_2PO_4^-$ (1 mM); its microelements were: Mn^{2+} (800 nM), Zn^{2+} (60 nM), Cu^{2+} (25 nM), Fe^{3+} (35 nM), BO_3^{3-} (160 nM), MoO_4^{2-} (50 nM).

2. Measuring of the production capacity of plants

The fresh and dry weights of the genotypes were measured per organs, in 4 repetitions, with 3 plants in each of it.

3. Sampling of leaves

The 5th developed leaf of each plant was detached at the end of a 8-hour dark period. A 3 cm pieces from each of the base and tip of the leaf, and the midrib were excised, and the homogeneous leaf-blade thus obtained was cut into 6 parts. The pieces of leaf were illuminated with a fluorescent lamp of 800 μmol · m^2 · s^{-1} light intensity for 1, 2, 5, 20, 60 minutes, respectively, under humid conditions at 24 °C temperature, 4 m · s^{-1} air flow and atmospheric CO_2 concentration, then immediately fixed in liquid air, and lyophilized.

4. Carbohydrate analysis

Soluble sugars were extracted from the dry matter with hot 70% ethanol; the extraction was repeated three times. From the collected fractions the soluble carbohydrates were determined with the phenol sulphuric-acid colorimetric method of DUBOIS *et al.* (1956).

In another part of the extract the monosaccharides were broken down with KOH at 90 °C (HANDEL 1968), then the quantity of the sucrose left (monosaccharides = soluble sugar — sucrose) was measured with phenol-sulphuric acid method.

From the pellet left after the ethanol extraction the starch was extracted with perchloric acid (350 g · dm^{-3}) (McCREADY *et al.* 1950); the extraction was repeated twice. The starch content of the extract was determined again with the phenol-sulphuric acid method mentioned above.

5. *Malate analysis*

From the aqueous extract prepared from the leaf (USUDA 1985) the malate was determined in an enzymatic way (HOHORST 1970).

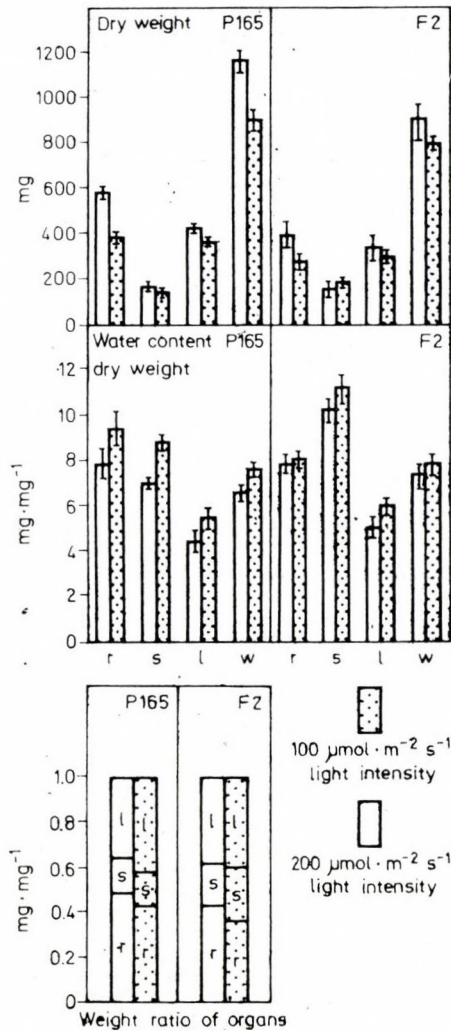



Fig. 1. Dry weight, water content and weight ratio of organs in 40 days old maize plants of genotypes P165 and F2 grown at two different light intensities. r: root, s: stalk (leaf sheath), l: leaf, w: whole plant

Results

1. *Characteristics of production capacity of the two maize genotypes*

1.1. Dry weight (Fig. 1)

Dry weights of organs of the P165 line are larger than those of line F2.
With the reduction of light intensity the dry weight of both the whole plant and its organs decreases, in P165 at higher and in F2 at lower degrees.

1.2. Dry weight ratios (Fig. 1)

The root/shoot ratio is higher in P165 than in F2 genotype.
In response to the reduction of light intensity the root/shoot raitos of genotypes P165 and F2 decrease at the same rate.

1.3. Water content (Fig. 1)

The water contents of the whole plant, its leaves and stalk are lower in P165 then in F2, while the water contents of roots are identical in the two genotypes.
With a decreasing light intensity the water content of the genotype P165 increases in a greater extent.

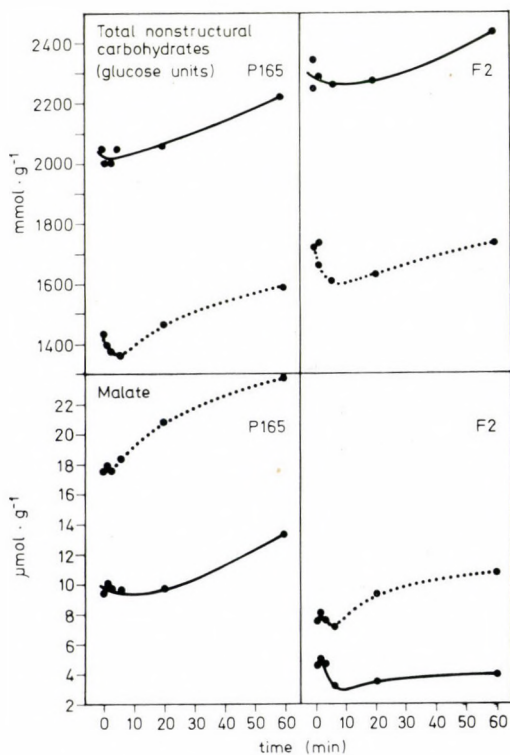



Fig. 2. TNC- and malate content in the 5th leaf of 40 days old maize plants of genotypes P165 and F2 growed at two different light intensities, illuminated with 800 μ mol · m^{-2} · · s^{-1} light intensity after acclimation in dark. ——— 200 μmol · m^{-2} · s^{-1}, — — — 100 μmol · · m^{-2} · s^{-1} light intensities plants treated with

2. *Metabolite levels in the 5th leaf at the end of the dark period*

The leaf of P165 contains less TNC, monosaccharide and starch, and more malate than that of F2, while the quantity of sucrose is nearly identical in the two genotypes.
The lower light intensity decreases the levels of TNC, monosaccharide and starch with 30–40 %, leaves the sucrose level unchanged, and increases the malate level by 70–80 %.

3. *Temporal changes in the metabolite levels of the 5th leaf in the first hour of the photoperiod*

3.1. Malate (Fig. 2)

Under the influence of light the level of malate decreases (for 0–10 minutes) first, then rises. In the P165 genotype the initial decrease is moderate. The rate of accumulation of malate in the 30th minute of illumination is more rapid in the P165 than in the F2 genotype at both light intensities.
The reduced light intensity shortens the first declining phase of malate content in both genotypes, and increases the rate of accumulation in the 30th minute of illumination.

3.2. Total non-structural carbohydrate (TNC) content (Fig. 2)

After an initial (2–8 min) decrease the TNC content gradually increases in both genotypes, at both light of intensities, at nearly the same rate. The reduction of light intensity increases the length of the declining phase.

3.3. Monosaccharides (Fig. 3)

The monosaccharide content becomes lower after 60 minutes of illumination. The monosaccharide level shows the following phases: declining (5–10 minutes)-, rising (10–20 minutes)-, constant (after 20 minutes) phase. In the declining phase of P165 the monosaccharide content decreases to a greater extent than in the F2 genotype.

3.4. Sucrose (Fig. 3)

The sucrose content increases from the beginning of the photoperiod. The increase can be divided in two phases: rapid (from the beginning of the photoperiod to the inflexion point of the curve) and slow (after the inflexion point of the curve) one. In the leaf of the P165 genotype the rapid phase of increase is shorter (14–16 minutes) than in that of the F2 genotype (23–25 minutes).
The reduction of light intensity shortens the rapid phase but increases the rate of sucrose accumulation in the 30th minute of the photoperiod.

3.5. Starch (Fig. 3)

After some decrease at the beginning of the photoperiod (7–15 minutes) the starch content gradually increases. The declining phase is shorter in P165 than in the F2 genotype.
The decrease in the intensity of light does not change the length of the declining phase.

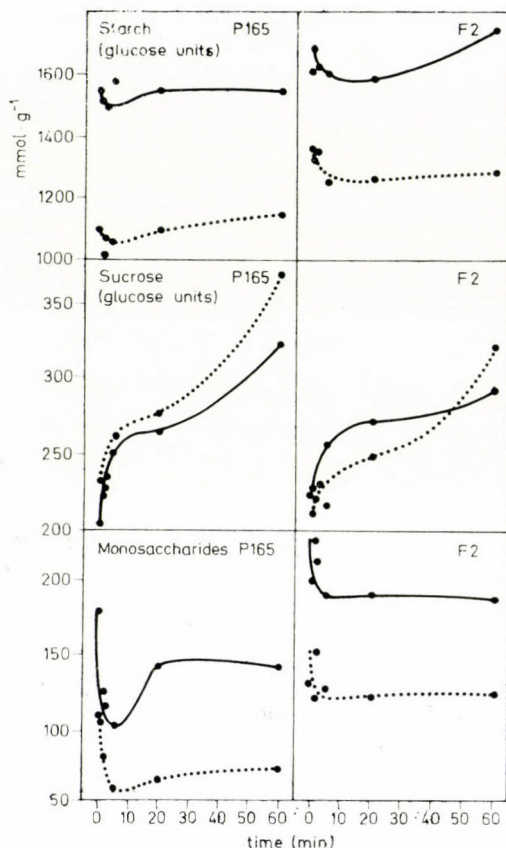



Fig. 3. Carbohydrate content in the 5th leaf of 40 days old maize plants of genotypes P165 and F2 grown at two different light intensities, illuminated with 800 μmol · m^{-2} · s^{-1} light intensity after acclimation in dark. ——— 200 μmol · m^{-2} · s^{-1}, and — — — 100 μmel · m^{-2} · · s^{-1} light intensitis

Discussion

1. Vegetative production of the two genotypes (Fig. 1)

The higher dry matter production of the P165 genotype confirmed by field experiments (Técsi 1984) suggests a more developed C4 NADP-ME type photosynthetic carbon reduction cycle. This shows that the PEPC and PPDK levels are in a closer correlation with the biomass than the RuBisCO level is (Sugiyama *et al.* 1984).

The genotype with higher vegetative production capacity was characterized besides the higher dry weight by a higher root/shoot ratio and lower water content which with the reduction of light intensity changed to a grea-

ter extent compared to the other genotype. The differences found between the plants of the two genotypes raised at higher and lower light intensities, respectively, showed the same tendency. Earlier examinations also indicated that unfavourable conditions (e.g. growing in short light-dark periods) brought the genotypes with higher productivity nearer to the genotypes with lower productivity (MARGÓCZI 1984).

2. *Metabolite levels of the 5th leaf at the end of the dark period* (Figs 2, 3)

The leaf of P165 contains more malate and less carbohydrate than the leaf of F2, supposedly being due to the higher ratio of PEPC/RuBisCO activity.

The ratio of PEPC/RuBisCO activity was studied in the tip-base region of the maize leaf, where a 50% increase of ratio was described (PERCHOROWICZ and GIBBS 1980).

The reduction of light intensity causes increase in the malate and decrease in the carbohydrate content, hence the malate forming system of the mesophyll cells is supposed to be less sensitive to limitations of light than the C_3 carbon reduction system of the bundle sheath cells.

The lower monosaccharide and starch content of P165 may possibly indicate a higher rate of respiration in dark or a more intensive utilization of monosaccharides and starch in growing, which fits in with the higher production potential.

The level of metabolites greatly depends on the availability of carbohydrates, particularly that of starch. The hydrolysis of starch supplies precursors for the synthesis of sucrose, while its phosphorolysis produces the precursors of the respiratory substrates (STITT *et al.* 1985). In the genotype F2 there is supposedly some obstacle to the utilization of the carbohydrate of the leaf.

The nearly identical sucrose level in the two genotypes indicates similar transport capacity (FADER and KOLLER 1983), which does not even change under the influence of lower light intensity. Other environmental changes, such as a decrease in the CO_2 content of air, cause less change in the sucrose than in the monosaccharide level (FOX and GEIGER 1984).

3. *Dynamic correlations of the metabolite level of the 5th leaf in the first hour of the photoperiod*

Malate (Fig. 2)

The initial malate synthesis is supposed to come from the aspartate reserves (COOMBS 1976, WILLIAMS and KENNEDY 1978). In the leaf of P165

genotype the rate of malate formation is higher than in the leaf of F2 in the 30th minute of the photoperiod.

The initial declining phase of the monosaccharide and starch level (5–15 minutes) is the period when these reserves are supposed to be utilized as inner sources of carbon, and serve the initial accumulation of the C_3 and C_4 metabolites (USUDA 1985). The fraction regarded as monosaccharides probably is mostly composed of stored carbohydrates rather than of Calvin intermediates.

For changes in the starch level partly the PGA/Pi regulation of the ADPG-pyrophosphorylase is responsible: on switching on the light the PGA/Pi ratio in the chloroplast increases and this starts the synthesis of starch. The latter is, however, greatly influenced by the cytoplasmic processes (e.g. sucrose synthesis) (PREISS 1982) as well as by a starch mobilization even demonstrable in light (FONDY and GEIGER 1985). It is thus easy to understand that the starch level only begins to rise after an initial decline.

Sucrose (Fig. 3)

The sucrose level shows immediate increase in response to light, in agreement with earlier experiences (SICHER *et al.* 1984). In the rapid phase of increase in the sucrose level (0–20 minutes) the sucrose produced is supposed to come from an inner source of carbon (monosaccharide, strach) rather than from the CO_2 fixation. In the subsequent phase (after 30 minutes) the accumulation of sucrose is due to the isolation of the leaf, i.e. the lack of export.

Metabolite ratios (Fig. 4)

The temporal change of the malate, starch and sucrose content relative to the monosaccharides is remarkably different in the two genotypes, but shows a similar trend as regards the light intensities under the plants were grown.

In genotype P165 these ratios show an intensive initial increase, then become evenly rising and constant, while in the F2 genotype they become evenly rising and constant after a slight decline at the beginning of photoperiod.

Under the influence of reduced light intensity under plants were growed the ratios increased in every case indicating that low light intensities have a decreasing effect on the relative quantity of monosaccharides.

As a final conclusion, the temporal changes of the studied metabolites show greater differences between the two genotypes than between the two light intensities. Thus, the induction period of photosynthesis is influenced

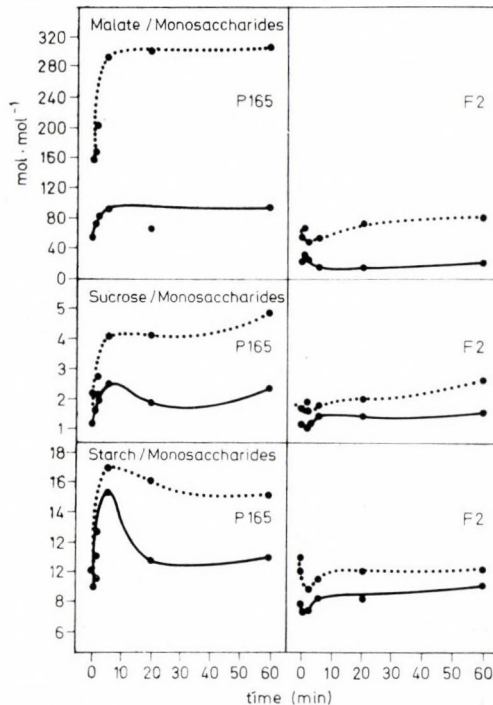



Fig. 4. Metabolite ratios in the 5th leaf of 40 days old maize plants of genotypes P165 and F2 growed at two different light intensities, illuminated with 800 μmol · m^{-2} · s^{-1} light intensity after acclimation in dark. ——— 200 μmol · m^{-2} · s^{-1}, and — — — — 100 μmol · m^{-2} · · s^{-1} light intensities plants treated with

to a greater extent by genetic factors than by environmental factors, e.g. light intensity.

ABBREVIATIONS

ADPG = adenosine-diphospho-glucose
DHAP = dihydroxy-acetone-phosphate
F1,6BPE = fructose-1,6-bisphosphatase (EC 3.1.3.11)
F2,6BP = fructose-2,6-bisphosphate
NADP-ME = NADP dependent malic acid enzyme (EC 1.3.1.40)
PEPC = phosphoenol-pyruvate-carboxylase (EC 4.1.1.31)
PGA = 3-phospho-glyceric acid
Pi = inorganic phosphate
RuBisCO = ribulose-1,5-bisphosphate-carboxylase (EC 4.1.1.39)
PPDK = pyruvate-phosphate-dikinase (EC 2.7.9.1)
SPS = sucrose-phosphate-synthetase (EC 2.4.1.14)
TNC = total non-structural carbohydrate

REFERENCES

Baer, G. R., Schrader, L. E. 1985: Stabilization of pyruvate, Pi dikinase regulatory protein in maize leaf extracts. *Plant Physiol.* **77:** 608–701.

Boag, S., Jenkins, C. L. 1985: CO_2 assimilation and malate decarboxylation by isolated chloroplasts from *Zea mays*. *Plant Physiol.* **79:** 165–170.

Coombs, J. 1976: Interactions between chloroplasts and cytoplasm in C4 plants. In Barber, J.: *The Intact Chloroplast.* Elsevier S.P.C., Amsterdam, New York, Oxford, 280–313.
Dubois, M., Gilles, K. A., Hamilton, J. K., Rebers, P. A., Smith, F. 1956: Colorimetric meth for determination of sugars and related substances. *Anal. Chem.* **28:** 350–356.
Fader, G. M., Koller, H. R. 1983: Relationship between carbon assimilation, partioning and export in leaves of two soybean cultivars. *Plant Physiol.* **73:** 297–303.
Fondy, B., Geiger, D. 1985: Diurnal changes in allocation of newly fixed carbon in exporting sugar beet leaves. *Plant Physiol.* **78:** 753–757.
Fox, T. C., Geiger, D. R. 1984: Effects of net carbon exchange on carbohydrate metabolism in sugar source leaves. *Plant Physiol.* **77:** 763–768.
Handel, E. 1968: Direct microdetermination of sucrose. *Anal. Biochem.* **22:** 280–283.
Hohorst, H. J. 1970: L(–)–Malat Bestimmung mit Malat-Dehidrogenase und NAD. In: Bergmayer, H. U.: *Methoden der Enzymatischen Analyse.* Academie Verlag, Berlin, 1544–1548.
Horváth, I. 1972: Phytotron in the Botanical Garden of the József Attila University, Szeged. *Acta Biol. Szeged* **18:** 15–19.
Huber, S. C., Rufty, T. W., Kerr, P. S. 1984: Effect of photoperiod on photosynthate partioning and diurnal rhythms in leaves of soybean. *Plant Physiol.* **75:** 1080–1084.
Jenkins, C. L., Boag, S. 1985: Isolation of bundle sheath cell chloroplasts from NADP-ME type C4 plant *Zea mays. Plant Physiol.* **79:** 84–89.
Margóczi, K. 1984: Effect of short light-dark periods on the morphology of hybrid maizes and their parent lines, and on the spatial and temporal distribution of carbohydrates in the leaves. Ph. D. Thesis, Szeged.
Maróti, I. 1986: Genotypic differences in the light adaptation changes of leaf chloroplast ultrastructure. *IVth Hungarian Symposium on Plant Anatomy.* Budapest, p. 18.
McCready, R. M., Guggols, J., Silviera, V., Owens, H. S. 1950: Determination of starch and amylase in vegetables. *Anal. Chem.* **22:** 1156–1158.
Pataky, S., Maróti, I. 1985: Connection of different photosynthetic activity with the structure of chloroplasts. *Hungarian—Austrian Joint Conference on Electron Microscopy* held together with XIIIth Hungarian National Conference on Electron Microscopy. Balatonaliga, p. 114.
Paz. N., Xu, D. P., Black, C. C. 1985: Rapid oscillation in fructose-2,6-bisphosphate levels in plant tissues. *Plant Physiol.* **79:** 1133–1136.
Perhorowicz, J. T., Gibbs, M. 1980: Carbon dioxide fixation and related properties in sections of the developing green maize leaf. *Plant Physiol.* **65:** 802–809.
Preiss, I. 1982: Regulation of the biosynthesis and degradation of starch. *Ann. Rev. Plant Physiol.* **33:** 431–454.
Sharkey, T. D., Berry, J. A., Raschke, K. 1985: Starch and sucrose synthesis on Phaseolus vulgaris as affected by light, CO_2, abscisic acid. *Plant Physiol.* **77:** 617–620.
Sicher, R. C., Kremer, D. F. 1985: Possible control of maize leaf sucrose-phosphate-synthetase activity by light modulation. *Plant Physiol.* **79:** 695–698.
Sicher, R. C., Kremer, D. F., Harris, W. G. 1984: Diurnal carbohydrate metabolism of barley primary leaves. *Plant Physiol.* **76:** 165–169.
Smyth, D. A., Black, C. C. 1984: The discovery of a new pathway of glycolysis in plants. *What's New in Plant Physiology* **15:** 13–16.
Sugiyama, T., Mizuno, M., Hayashi, M. 1984: Partioning of nitrogen among ribulose-1,5-bisphosphate-carboxylase/oxygenase, phosphoenolpyruvate carboxylase, and pyruvate-orthophosphate-dikinase as related to biomass productivity in maize seedlings. *Plant Physiol.* **75:** 665–669.
Stitt, M., Wirtz, W., Gerhardt, H. W., Spencer, C., Walker, P., Foyer, C. 1985: A comparative study of metabolite levels in plant leaf material in the dark. *Planta.* **166:** 354–364.
Técsi, L. 1984: Anatomical comparisons of leaves of maize lines and their hybrid, analysis of photosynthetic pigments and malate. *Professional Dissertation.* Szeged, József Attial University.
Usuda, H., Ku, M. S., Edwards, G. E. 1984: Activation of NADP-malate-dehydrogenase, pyruvate, Pi dikinase and fructose-1,6-bisphosphate in relation to photosynthetic rate in maize. *Plant Physiol.* **76:** 238–243.
Usuda, H. 1985: Changes in levels of intermediates of the C4 cycle and reductive pentose-phosphate pathway during induction of photosynthesis in maize leaves. *Plant Physiol.* **78:** 859–864.
Williams, L. E., Kennedy, R. 1978: Photosynthetic carbon metabolism during leaf ontogeny in *Zea mays* L. In: Enzyme Studies. *Planta.* **142:** 269–274.

Acta Botanica Hungarica 33 (3—4), pp. 431—436 (1987)

HEMOLYTIC SAPONIN CONTENT OF HERBAGE

J. VETTER and E. HARASZTI

DEPARTMENT OF BOTANY, UNIVERSITY OF VETERINARY SCIENCES, BUDAPEST

(Received: 25 January 1986)

The authors carried out quantitative determinations of saponin content in papilionaceous-, grass- and other species of grasslands for 143 samples of a total of 80 species. Besides species of the genus *Medicago* (*Medicago sativa*, *M. lupulina*, *M. falcata*) saponin was measured in the species *Anthyllis vulneraria* and *A. macrocephala*, and in all samples of *Astragalus cicer* (while the other A. species proved negative). Of the grass species examined *Arrhenatherum elatius* while of the other species *Melandrium silvestre* were the only ones that contained considerable quantities of saponin. Our data point to a relationship between the saponin content and the development of plant. It was found that the range of our major saponin bearing plants was wider and more diversified than thought so far, and that beside the effects of growing site first of all genetic and physiological factors played important role in determining the saponin level in plants. It is remarkable that of our grass species onion couch, a major component of our grasslands considered valuable from other points of view (drought tolerance, yield) is the one that contains a large amount of saponin.

Introduction

Saponins are rather widely distributed in the flora. Earlier data mention 500 species from 80 families that contains saponins (BASU and RASTOGI 1967). (Plants known to contain saponins are: *Digitalis* sp., *Aesculus hippocastanum*, *Aralia* sp., *Glycyrrhiza glabra*, *Gypsophila* sp., *Avena sativa* (avenacin), *Helianthus annuus*, *Phytolacca americana*, *Anemone-*, *Polygala-*, *Primula* sp., *Sophora japonica*, *Hedera* sp., *Panax ginseng*, *Anchusa officinalis*, etc.)The saponins are glycosides whose aglycons, the sapogenins are polycyclic systems of steroid- (C_{27}) or triterpenoid (C_{30}) character. Their most conspicuous effect is the hemolysis of erythrocites following the increased permeability of the cell membrane. The saponins act on the foaming processes in the rumen, inhibit certain enzymes (α-kymotrypsin, proteases), exercise a negative effect on some insects and fungi (*Trichoderma* sp.) and on the germination of certain plant seeds (BONDI *et al.* 1973). The lucerne meal e.g. which has a high saponin content slows down the weight increase of chickens to a considerable extent. In the case of lucerne — as the most important saponin-bearing plant — medicagenic acid is thought to be primarily responsible for the negative biological effect. Recent investigations have dealt with the steroid saponins of Trigonella foenum-graecum (VARSHNEY *et al.* 1982), with furastanol glycosides in the seeds of the latter plant (GUPTA *et al.* 1984), and with questions of the hemolytic effect (ELMADFA and KOKEN 1980). Botanical researches try to answer the question of what the role of steroid saponins localized in the etioplasts and chloroplasts of Avena sativa in the process of greening is (KESSELME and URBAN 1983, KESSELME 1982). Investigations have been made into the insecticide (Taenia coli: TAKAHASHI and CHUJYO 1984) and fungicide (Pythium: DEACON

Table 1

Grassland species examined for hemolytic saponin content and found negative (in brackets the number of samples if more than one)

1. Grasses (Gramineae)

Agropyron repens P. B.
Alopecurus geniculatus L.
A. pratensis L. (2)
Anthoxanthum odoratum L.
Bromus erectus Huds.
B. inermis Leyss.
B. mollis L. (3)
Dactylis glomera a L. (7)
Festuca arundinacea Schreib.
F. pratensis Huds.
F. pseudovina Hackel ap. Wiesb. (4)
F. rubra L.
F. rupicola Heuff. (4)
Holcus lanatus L. (2)
Lolium multiflorum Lam.
Melica uniflora Retz.
Poa nemoralis L.
Poa pratensis L. (6)
Poa trivialis L.
Typhoides arundinacea (L.) Dum.

2. Legumes (Papilionaceae)

Astragalus asper Wulf.
A. austriacus Jacq.
A. glycyphyllus L. (6)
A. onobrychis L.
Coronilla varia L. (3)
Dorycnium herbaceum Vill.
Hippocrepis comosa L.
Lathyrus pratensis L.
Lotus corniculatus L. (3)
Melilotus albus Desr. (2)
M. officinalis Lam. (3)
Onobrychis viciifolia Scop. (3)
Ononis spinosa L. (2)
Tetragonolobus maritimus L. Roth ssp. siliquosus (L.) Murb. (2)
Trifolium alpestre L.
T. campestre Schreib. (2)
T. incarnatum L.
T. montanum L.
T. pratense L. (8)
T. repens L. (5)
Vicia angustifolia Grufbg.
V. hirsuta (L.) Gray
V. pisiformis L.

3. Weed species

Achillea collina L. Becker
Ajuga genevensis L.
Alliaria petiolata (M. B.) Cavara et Grande
Artemisia vulgaris L.
Cephalaria transsilvanica L. Schrad.
Cruciata glabra (L.) Ehrend
Euphorbia cyparissias L.
E. esula L.
Galium glaucum
G. mollugo L.
G. schultesii Vest.
G. verum L.
Lepidium drab Desr.
Pastinaca sativa L.
Peucadenum palustre (L.) Mnch.
Ranunculus acris L.
R. polyanthemos L.
Rhinanthus minor L.
Rumex acetosa L. (2)
Salvia nemorosa L.
S. pratensis L.
S. verticillata L.
Sanguisorba officinalis L.
Stellaria holostea L.
Thymus glabrescens Willd.
T. marschallianus Willd.
Veronica chamaedrys L.

The plant samples included in the study were collected from the following places: Ecseg (Nógrád county), Kelemér (Borsod-Abaúj-Zemplén (BAZ) c.), Aggtelek (BAZ c.), Szalonna (BAZ c.), Kunszentmiklós (Bács c), Szabadszállás (Bács c), Mórahalom (Csongrád c), Dömsöd (Pest c.), Pilisszentlélek (Pest c), Nova (Zala c), Zalabaksa (Zala c.), Vácrátót (Pest c), Sződliget (Pest c).

and Mitchell 1985) effect of some saponins, or on their role in preventing hypercholesterolaemia (Malinov *et al.* 1981).

Researches in Hungary have mainly focussed on phytochemical aspects (Held and Vágujfalvi 1967), and methodological questions of saponin determination in lucerne (Majkó 1978, Fehér 1983, Fehér and Lőrincz 1983), or on the relation of lucerne breeding and saponins (Buglos and Bócsa 1976), or evaluated certain species of the Hungarian flora from the point of view of crude protein-, alkaloid-, sterol- and saponin content (Koch *et al.* 1969).

We set the objective of demonstrating the presence and determining the quantity of hemolytic saponins in samples of herbage species obtained from various habitats in Hungary. Our objective is supported by the following reasons: the number of studies carried out in this field in Hungary for the last two decades is small; with the development of grass vegetation and pasture management increased demands are raised on quality, and detecting the saponin-bearing plants satisfies an important practical demands, since they undoubtedly reduce the value of fodders (they have a so-called "antinutritive" effect). Our data are hoped to supplement our rather deficient knowledge of the range of saponin-bearing plants.

Material and method

From all sites of sampling grass-, papilionaceous- and other (weed) species characteristic of the respective grasslands were collected in 1985. The places of sample collecting are named at the foot of Table 1. The hemolytic saponin content was determined from the carefully dried and ground plant material after the method of Majkó (1978). The plant material was extracted with a 0.9% solution of NaCl in shaker. After it had been filtered and centrifuged the pure supernatant was tested for hemolytic reaction with swine blood in centrifugal tube (reaction time: 1.5 hour at room temperature). As a modification of the original method 0.75 ml 20% Na-citrate solution wass added to the reaction mixture to counterbalance the Ca content generally not to be neglected in the extracts (the composition of the mixture was thus: 5 ml extract + 0.75 ml 20% Na-citrate + 0.5 ml swine blood). After centrifuging the extent of hemolysis was evaluated by spectrophotometry at 600 nm. Calibration was carried out with Merck's saponin solution and the hemolytic saponin content of the plants was evaluated on the basis of the curve obtained.

Results

A list of the species which with our method were not found to contain saponins is given in Table 1. The sensitivity of our method enabled us to demonstrate a saponin content of about 0.5–0.6 g/kg dry matter, and the reason why its sensitivity cannot be increased is that demonstrable hemolysis only appears at a saponin concentration of about 30 μg/ml. It is interesting that among the species listed in Table 1 there are important and frequent papilionaceous components of grasslands, such as species of the *Trifolium* genus, *T. pratense*, *T. repens* and *T. montanum*, *Vicia* and *Melilotus* species, *Lotus corniculatus*, *Coronilla varia*, *Tetragonolobus maritimus*, several *Astragalus* species, etc. The large number of grass species examined represented a good many genera, and from certain species more sample were analysed (e.g. 7 of *Dactylis glomerata*, 6 of *Poa pratensis*, 4 of *Festuca rupicola*). Species examined but found negative for hemolytic saponin content include: *Ajuga genevensis*, *Alliaria petiolata*, *Euphorbia-*, *Galium-*, *Ranunculus-*, *Salvia-*, *Thymus-*, *Veronica* species, etc. The table records the examination of 122 samples of a total of 72 species.

The average saponin contents of species found positive for hemolytic saponins are given in Table 2 in g/kg dry matter and g/kg fresh plant. The second growth of alfalfa (*Medicago sativa*) contained 1.27–2.94 g/kg dry matter saponin, which according to Majkó (1978) and Fehér and Lőrincz (1983) is regarded as a low saponin content. Similar saponin content was

Table 2

Values of hemolytic saponin contents

	Hemolytic sampions	
	g/kg dry matter	g/kg fresh plant
Medicago sativa L.		
Gödöllő, aftercrop 14 May	2.32	0.42
Gödöllő, aftercrop 4 June	2.94	0.53
Soroksár, aftercrop	1.27	0.23
Medicago lupulina L.		
Vácrátót, in flower	2.10	0.38
Szabadszállás, in flower	1.23	0.22
Szalonna, in flower	1.42	0.26
Medicago falcata L.		
Aggtelek, aftercrop	5.73	1.04
Anthyllis vulneraria L.		
Gödöllő, aftercrop 14 May	11.0	2.0
Gödöllő, in flower	1.99	0.36
Anthyllis macrocephala Wenderoth		
Aggtelek, in flower	3.96	0.72
Astragalus cicer L.		
Vácrátót aftercrop	1.42	0.26
Sződliget, in flower	1.18	0.22
Kelemér, aftercrop	1.47	0.26
Szabadszállás, aftercrop	1.26	0.23
Szeged—Baja, aftercrop	1.08	0.19
Arrhenatherum elatius (L.) Presl.		
Sződliget, in flower	6.0	1.81
Gödöllő, in flower	4.9	1.49
Szalonna, in flower	5.3	1.61
Pilisszentlélek, in flower	6.3	1.93
Ecseg, in flower	12.6	3.83
Melandrium silvestre (Schkuhr.) Röhling.		
Pilis, in flower	8.9	1.64

measured in *Medicago lupulina* samples obtained from 3 growing sites (1.23–2.7 g/kg dry matter). The only relevant report by Koch *et al.* (1969) confirms the hemolytic saponin content of *Medicago minima* and *M. lupulina*, though the mentioned authors only carried out qualitative demonstration. The second growth of *Medicago falcata*, the third *Medicago* species examined, showed a much higher saponin content (5.7 g/kg dry matter).

Anthyllis vulneraria, one of the species analysed from the genus *Anthyllis*, could be examined in two stages of development: the aftercrop was characterized by a very high (11.9 g/kg dry matter) saponin content, while at the flowering stage the saponin content was as low as 1.99 g/kg dry matter. Considering that the two samples were obtained from the same plant stand it seems likely that in the course of development the saponin content undergoes great changes within a short time. These data unanimously confirm Buglos and Bócsa's

(1976) statement of a decrease in saponin level during the development of alfalfa, resulting by the very time of flowering in a relatively low saponin content. The comparatively high saponin content of the genus *Anthyllis* is otherwise indicated by the nearly 4 g/kg dry matter saponin content found in the flowering sample of *A. macrocephala*, the other species examined from the genus. The saponin-bearing character of the species was suggested by KOCH *et al.*, too.

Among the species analysed from the genus *Astragalus* only *A. cicer* — but then all its samples — was found to contain saponins, though not too much (1.0–1.47 g/kg dry matter). These values agree with the data of KOCH *et al.* (1969), though the latter found considerable quantities of saponins in *A. austriacus*. In our analyses neither *A. austriacus* nor the other *Astragalus* species (represented by 15 samples) proved to contain saponins in quantities exceeding the level of traceability. The deficiency of our knowledge concerning the saponin content of papilionaceous crops is also indicated by the fact that in the present series of analysis saponins were not traced in any of the *Trifolium* samples examined, while the aforementioned authors found hemolytic saponin in *T. alpestre* before flowering, though in no samples of *T. dubium*, *T. montanum*, *T. rubens* and *T. strictum* could they point it out.

The samples of onion couch (*Arrhenatherum elatius*) taken at the stage of flowering showed considerable saponin contents (5–12 g/kg dry matter) for all growing sites examined. This saponin concentration — very high even in comparison to the papilionaceous species — was the highest among those found in any of the species examined. Saponins in the other grass species examined, some of which were represented by quite a few samples (*Poa pratensis*, *Bromus mollis*), did not reach the level of traceability by our method. It is interesting that KOROHODA and WITKOWSKA (1969) found the rye-grass to give positive reaction to tests.

Of the weed species analysed Melandrium silvestre from the family Caryophyllaceae was the only one that prove saponin bearing (8.97 g/kg dry matter). This value agrees with the data of KOCH *et al.* (1969) concerning the saponin-bearing nature of the family, although the mentioned authors found both saponin-containing and saponin deficient species within the same genus.

REFERENCES

Basu N., Rastogi R. P. 1967: Triterpenoid saponins and sapogenins *Phytochemistry*, **6:** 1249—1270.

Bondi A., Birk Y., Gestetner B. 1973: Forage saponins. In: *Chemistry and Biochemistry of Herbage* (Ed.: Butler G. W., Bailey R. W.) Academic Press, London—New York, 511—528.

Buglos J., Bócsa I. 1976: A lucerna szaponintartalmának csökkentésére irányuló nemesítés kérdései (Questions of breeding for reduced saponin content in alfalfa) *Növénytermelés*, **25/4:** 335—343.

Deacon J. W., Mitchell R. T. 1985: Toxicity of out roots, oat root extracts and saponins to zoospores of *Pytium* spp. and other fungi. *Tr. Br. Mycol.* **84:** 479—487.

Elmadfa I., Koken M. 1980: Influence of vitamin-E and the protein quality on the hemolytic effect of Trigonella sapogenins in rats. *Z. Ernährung* **19/4:** 280—289.

Fehér F. 1983: A lucerna össz-szaponintartalmának közelítő meghatározása hemolitikus módszerrel (Approximative determination of total saponin content in alfalfa by hemolytic method) *Növénytermelés*, **32/6:** 509—512.

Fehér F., Lőrincz A. 1983: A lucerna hemolitikus szaponintartalmának gyors mennyiségi meghatározása (Quick quantitative determination of hemolytic saponin content in alfalfa). *Növénytermelés*, **32/3:** 219—224.

Gupta R. K., Jain D. C., Thakur R. S. 1984: Plant saponins 6. Furastanol glycosides from *Trigonella foenum-graecum* seeds. *Phytochem.* **23/11:** 2605—2607.

Held Gy., Vágújfalvi D. 1965: A *Tamus communis* L. szteroid-szaponinjainak vizsgálata (Study of steroid saponins in *Tamus communis* L.) *Bot. Közlem.*, **52/4:** 201—205.

Kesselme J., Urban N. 1983: Subcellular localization of saponins in green and etiolated leaves and green protoplasts of oat (*Avena sativa* L.). *Protoplasma*, **114/1—2:** 133—140.

Koch B., Boros Á., Szabó L. 1969: A magyar flóra néhány fajának nyersfehérje-, alkaloida-, szterol- és szaponintartalma takarmányérték szempontjából (Crude protein-, alkaloid, sterol and saponin contents in some species of the Hungarian flora from the point of view of feed value). *Agrobotanika*, **11:** 124—140.

Korohoda J., Witkowska A. 1969: Wstepne badania nad wysteponaniem saponin w koniczynie, lucernie i trawach. *Zesz. Probl. Post. Nauk Rolniczyh.* **80:** 105—107.

Majkó Z. 1978: Hemolitikus hatású szaponinok mennyiségi meghatározása lucernában (Quantitative determination of hemolytic saponins in lucerna). *Növénytermelés*, **27/3:** 217—222.

Malinow M. R., Mclaughl P., Stafford C., Livingston A. L., Kohler G. E. 1981: Prevention of hypercholesterolemie in Macaca fascicularis. *Arterioscle.*, **1/1:** 59.

Takahashi S., Chujyo N. 1984: Treatment of Taenia coli with saponin. *Jap. J. Pharm.* **36:** 179.

Varshney J. P., Jain D. C., Beg M. F. A. 1982: Steroidal saponins from *Trigonella foenum-graecum* L. *J. Steroid B.* **17/3:** 69.

Acta Botanica Hungarica 33 (3—4), pp. 437—451 (1987)

BOOK REVIEWS

Editor: G. Fekete

M. Zohary: Plants of the Bible. Cambridge University Press. 1982, pp. 208.

Archbishop Haynald, who wrote his doctoral thesis on the plants of the Bible, and many other botanists were concerned with the plants occurring in the gospel (e.g. Celsius 1748, Boissier 1861, Moldenke 1952). Dr. Zohary, the late professor of Botany at Hebrew University, Jerusalem, a noted expert of the topic and the editor of the flora of Israel, presents a new approach based on the most recent results. In addition to the enumeration of plants according to the most recent taxonomy, he draws a picture on the potential original flora and vegetation of the land of the Bible. Two hundred excellent colour photographs supplement the text.

The first section points to the ecological aspects of the relationship between the man of the biblic times and his environment. The role of plants in their religious belief and life, and the significance of cultivated plants in the everyday life of the people are discussed. The author was the member of the Academy of Sciences of Israel, and he had been involved in botanical studies of the area for half a century. Thus, he treats very thoroughfully and carefully the difficult problem of identifying plant species of the Bible. His conclusions are supported by new results of floristic studies, and topographical, ethnobotanical and geobotanical observations. The most important vegetation types and the influence of climatic factors, mainly the most decisive change of seasons, are described. Written evidence and material proof support statements on the primary role of former trade routes, the Jewish culture, traditional folk medicine and customs, and art. In the second part, each plant is described in separate units. The analysis of Greek and Hebrew names in the italicized citations is followed by a systematic evaluation, the clarification of complex relationships, the review of recent views, and suggestions. Then, present day significance, use and cultivation of the plant are discussed. Although the species are grouped according to their ecological requirements, the Index facilitates easy orientation in the book. The text is supplemented with a short morphological glossary, bibliography, index of English and Latin names, and a comprehensive list of citations from the Bible.

The botanical analysis of the Bible contributes much to our knowledge on this fundamental book of Christianity and European culture. The readable style and the contents of this book, which is free from any pseudo-scientific and religious prejudices, may be of interest primarily for believers for whom the message in the gospel will be illuminated from a completely new viewpoint, and also for anybody dealing with botany or simply intending to get an insight into the scientific study of the Bible.

Z. Kereszty

O. L. Lange, P. S. Nobel, C. B. Osmond, H. Ziegler (eds): Physiological Plant Ecology II. Water Relations and Carbon Assimilation. In: Encyclopedia of Plant Physiology. New Series, Vol. 12 B., Springer-Verlag, Berlin–Heidelberg–New York, 1982, pp. 747, with 153 Figures.

The book consists of 18 chapters, an author index, a taxonomic index and a subject index on 747 pages, with 153 figures.

The topic of chapter 1 is water in the soil-plant-atmosphere continuum. First, what is

meant by the water status of plant is discussed. Then it is shown how the water status is influenced by short term processes and how the long-term processes influence the water relations and photosynthetic productivity.

In chapter 2, "Water in tissues and cells", the components of tissue water potential (ψ), the osmotic potential (π), analysis of isotherms, the pressure potential (β), cell-wall elasticity and plasticity, apoplasmic water, ecological implications of tissue-water potential characteristics, bulk modulus of elasticity (ε), turgor maintenance and growth, cell size and resurrection plants are included, providing us with much new and useful information.

In chapter 3, "Water uptake and flow in roots", the features of this system are in the focus and discussed in detail: a) the hydraulic resistance of the root, b) the pathway through the root, c) the hydraulic resistance of the soil up to the surface.

The fourth study gives an overview on the foliar uptake of water by flowering plants in arid zones (bromeliads, orchids, poikilohydric angiosperms, ferns and fern allies). It deals with the water uptake by bryophytes and lichens. An evolutionary perspective of adaptive mechanisms is far too frequently ignored in recent investigations.

Chapter 5, "Transport and storage of water" consists of two parts. The first describes the structural basis of water conduction from roots to leaves, the second concerns water storage in the plant body, a property widely varying among species.

Chapter 6 summarizes the results of investigations on the resistance of plant surfaces to water loss, such as transport properties of cutin, suberin and associated lipids. Excellent electron micrographs of plant cuticles supplement the text.

Chapter 7 attempts a comparative analysis of the operational range of leaf conductance and CO_2 assimilation rate, the regulation of these processes. It includes an analysis of the relationship between stomata, plant wa ter loss and plant water status.

Chapter 8 deals with the mathematical models of plant water loss and plant water relations. The analysis is restricted to homeohydric plants. The authors' aim is to provide a conceptual basis for the development of models which predict water loss from plants reliably.

Chapter 9 discusses the physiological responses to moderate water stress (specific water-related parameters for quantifying plant water status) and briefly considers how changes in the parameters may affect plant functions.

Chapter 10, "Desiccation-tolerance", gives us some interesting information on the taxonomic origins of desiccation-tolerance in higher plants, theories of desiccation-tolerance, as well as on the cellular responses of tolerant and intolerant plants to desiccation and rehydration. Finally, the conclusion can be drawn that different species have developed different ecological, morphological and physiological adaptations to accomplish a net gain in their photosynthetic productivity.

Chapter 11 deals with frost-drought and its ecological significance, including water uptake and conductance (soil frost, temperature dependence, etc.) water loss, water balance and winter stress injuries.

In chapter 12, we can get acquainted with the germination processes in seeds, seed-water relations during germination, statics and dynamics of seed-water relations, pathways for water entry into the seed, and optimalization of water supply.

Chapter 13, "Environmental aspects of the germination of spores", deals with the functions of spores and the enhancement of survivability and dissemination and their use as timing devices.

Chapter 14 discusses the physiological responses to flooding, including the symptoms, causes of injury, the different survival mechanisms and the evolution of flooding tolerance.

The main purpose of chapter 15 is to attempt a critical evaluation of the large-scale experiments of nature, presenting the photosynthetic response to seasonal and geographic climates, and the distribution of plants with different photosynthetic pathways. The title of the chapter is "Functional significance of different pathways of CO_2 fixation in photosynthesis".

Chapter 16 gives an account of modelling of photosynthetic response to environmental conditions. It discusses in detail stromal and extrachloroplastic reactions, thylakoid reactions, integration of factors limiting RuP_2 regeneration, integrated C_3 metabolism, long-term effects on leaf photosynthesis, C_4 pathway, canopy photosynthesis and some empirical methods.

In chapter 17, "Regulation of water use in relation to carbon gain in higher plants", the authors try to support the theory that selective adaptations have tended to "optimize" the relationship. A theory of short-term regulation and longer-term regulation is in the focus.

The last chapter gives us a very useful survey of the plant life forms and their carbon, water and nutrient relations. The author (D. E. SCHULZE) tried to make assumptions about the "strategies" by which different plant life forms may operate. After the investigations they are still at the level of asking "what plant life forms do" instead of "why plant life forms do".

At the end of each study extensive references, are presented.

Providing plenty of information, it is an essential, high-standard handbook which is very useful for all scientists dealing with eco-physiology.

Z. Tuba

W. Braune, A. Leman and H. Taubert: Pflanzenanatomisches Praktikum I. Einführung in die Anatomie der Vegetationsorgane der höheren Pflanzen. 3rd revised edition. VEB Gustav Fischer Verlag, Jena. 1979. 311 pages.

The authors present a knowledge accumulated during their long practice in education and research. The book is helpful for botanical courses, as well as for basic and applied research work in the field of plant cell biology and histology. It is a well-edited and well-structured handbook.

The material necessary for plant anatomical studies is divided into parts following the classic subdivision. The main chapters are as follows: the microscope, the use of microscope, the plant cell (protoplasm, mineral parts), the organization of cells (meristem, mature tissues), plant organs (shoot, leaf, root), methodological index, list of references, and subject index. The register on the page margins promotes quick orientation in the book, it refers to the discussion of main topics: cell, shoot, leaf, and root.

As an introduction to major chapters, the detailed discussion is preceded by a concise theoretical part focusing on the most important terms (e.g. cytoplasm, plastids, meristems, mature tissues, shoot, cambium, secondary phloem, leaf, leaves of gymnosperms and angiosperms, primary roots, development of central cylinder, etc.).

The greatest value of the book is the very rich selection of photographs and diagrams. The 94 figures, composed of 417 small inserts, promote the understanding of details and the recognition of basic relationships, even though the high-quality paper is perhaps too shining. Especially good pictures are those showing protoplasmic streaming in the cells of squash (*Cucurbita pepo*), leaf cross sections of beech (*Fagus silvatica*) and longitudinal sections of the shoot of squash. There are excellent micrographs and figures on the palisade parenchyma of lilac (*Syringa vulgaris*) the cross section of the twigs of small-leaved lime (*Tilia cordata*) and the cross section of the root of nettle (*Urtica dioica*), respectively. Most of the photographs are original; these are supplemented with diagrams drawn to scale. This arrangement and the straightforward explanations on the diagrams greatly facilitate quick identification of details when working with a microscope.

The standardized plans of studies is another advantage of the book. At the beginning of each subject, the objective of the study is determined and then the following terms, subtitles are presented (in that order):

a. material (name of plant, the plant part to be examined, type of tissue),
b. method of preparation (the preparation of excisions, chemicals to be used),
c. other methods of preparation,
d. observations (references to pictures and explanations to figures),
e. other observations (short explanations that do not relate directly to the primary objective of the study),
f. errors and artefacts (deformations during preparation, inadequate techniques of cutting tissue sections), and
g. other materials worth examining (e.g., those offering the study of similar organelles and tissues).

The last chapter of the book is an alphabetic index of materials, tools, chemicals and methods for cytological and histological work. Each laboratory study includes a section on the "Technique of preparation" in which reference is made to the chemicals and the preparation technique as listed in the index.

The bibliography on botanical laboratory handbooks and on microscopic techniques seems a bit incomplete, although 66 books, mainly in English and German, are listed.

Even though this third edition appeared in 1979, it is a very useful and modern handbook, thanks mainly to the very rich illustrative material.

L. Kaszab

Elena MASAROVICOVÁ: Gasometrical Investigation into CO_2 Exchange of the Fagus silvatica L. Species Under Controlled Conditions (Gazometrické studium vymeny CO_2 druhu Fagus silvatica L. v kontrolovanych podmienkach). VEDA, Publishing House of Slovak Academy of Sciences, Bratislava, 1985, pp. 116.

The present book provides an excellent up-to-date review of photosynthesis ecophysiology in woody species, a detailed comparative description of the CO_2 gas exchange methods and basic new results of C-balance in European beech.

This volume gives new data on photosynthesis, photorespiration and mitochondrial respiration processes of young beech trees (*Fagus silvatica* L.) stemming from the natural forest stand at one of the research areas in the Malé Karpaty Mountains (Slovakia).

The volume consists of six chapters, a list of abbreviations, symbols, units and conversion coefficients used, a list of literature cited (268 items) and a summary in English, Slovakian and Russian.

In the introduction (Chapter 1) the author — among others — emphasizes that the basic data provided by the present investigations under controlled conditions, apart from general significance of scientific information, are also applicable to the development of models of C-balance of woody tree species under natural conditions.

The second chapter, "The contemporary state of the art", is divided into nine subchapters. The first subchapter deals with the growth and development of seedlings (shoot growth and ontogenetic development and structure of the leaf). In the next subchapter we can get an overview of the complex of internal and external factors, which acts upon the photosynthesis and respiration of woody species. It deals with the radiatilon flux density (irradiance), temperature, water, genetic factors and the ontogenetic seasona changes.

The next part of the chapter explains the use of the term "potential photosynthetic rate". Then, it deals with the CO_2-curves of net photosynthetic rate (P_N), the inhibitory effect of oxygen upon photosynthetic rate as well as the effect of light intensity and temperature.

In the following parts of the chapter we can get useful information about the CO_2 compensation concentration which is a sensitive parameter for appraising the photosynthetic plant activity, general characteristics of photorespiration (relative to photosynthesis and C_3, C_4 species), mitochondrial respiration (dark respiration, R_D) general characteristics and significance in metabolism relative to photorespiration) and finally about the feasibility of rising potential production by respiration regulation.

Chapter 3 describes the material and the applied methods. First of all, we can get some information about the geographico-geological, pedological, climatic and vegetational conditions of the study site in the Malé Karpaty Mountains (South-west Slovakia). We can also read about the experimental material (the investigated species), which were 3 year old airborne young plants of the European beech (*Fagus silvatica* L.).

The subchapter "Methods applied" discusses the advantages and drawbacks of the gravimetric and gasometric methods of photosynthesis measurements and deals with the analysis of the open and closed system used. Furthermore, much attention is paid to the method of photorespiration measurement, including CO_2 concentration measurement and flowing gas desiccation. After that the description of the measuring equipment, the used assimilation chamber construction and the whole measuring apparatus is given. One of the greatest value of this book is the detailed, correct description of the gasometric methods used. The author presents also the parallell measured most important micrometeorological factors, such as irradiance, air temperature and humidity and she describes the way of the leaf surface temperature measurements.

The numerical and statistical evaluation of the results is given in the third chapter. Methods used here include graphical correlation and regression analysis.

Chapter 4 describes the results. It deals with the growth and development of young European beech, with the anatomy (leaf mesophyll structure) of leaves and their ultrastructure (peroxisomes and chloroplasts), with photosynthetic activity and photorespiration activity of physiologically adult leaves, with the mitochondrial (dark) respiration rate as a function of temperature and oxygen concentration, with parameters characterizing *Fagus silvatica* as a C_3 species, seasonal curves of the investigated quantitative ecophysiological characteristics (net and gross photosynthesis rate, photosynthetic production, mitochondrial respiration rate, photorespiration rate CO_2 compensation concentration) and finally with the balance of assimilation and dissimilation processes in the light and in the dark.

The fifth chapter contains the exact, detailed discussion of the results. The last chapter gives a very good summary of the concepts and results of the whole investigation.

From the new results here I would like to cite that 1) the young European beech has

a relatively high value of the CO_2 compensation concentration, and 2) the young beech species possess a relatively high photorespiration rate and mitochondrial respiration rate in the dark.

One of the greatest merit of this study — apart from the results — is that the methods applied may be utilized not only in the investigation of the ecophysiological features of woody and other plants, but on a wider scale, e.g., within the applied forest research, too.

This book, based on a wide range of investigations, provides plenty of new information. It is well-supplied with figures and photos. The general presentation of material is of a high standard.

This valuable study should not be absent from botanical libraries and it can be highly recommended to everybody dealing with plant ecophysiology.

Z. TUBA

Morris LIEBERMAN (ed.): Post-harvest Physiology and Crop Preservation. NATO Advanced Study Institutes Series, Series A: Life Sciences, Vol. 46. Plenum Press. New York and London, 1983, pp. 572.

This book is the 46th volume of the well-known and popular series: Life Science and Records the Proceedings of the NATO Advanced Study Institute on Post-Harvest Physiology and Crop Preservation held at Sounion, Greece, April 28–May 8, 1981.

The book is divided into 7 parts. The first part is an overview of the biochemistry and physiology of senescence. The first chapter of this part deals with the general biology of plant senescence and the role of nucleic acids in protein turnover in the control of senescence processes, which are genetically programmed.

In the next chapter, the control mechanisms of ribonucleic acid and enzyme synthesis during fruit ripening are described. It discusses the problems of polygalacturonase synthesis during ripening and the relationship between the synthesis of ethylene and polygalacturonase.

The following chapter deals with the respiration and energy metabolism in senescing plant tissues. The author examined the rate of production, regulation and physiological significance of metabolic energy in these tissues. The rise in respiration intensity during senescence of fruits, leaves and cut flowers may not reflect the increased energy requirements of senescence processes.

The chapter entitled "Enzyme activities and postharvest change" describes some of the potential mechanisms available for the in vivo regulation of enzyme activity.

In the next chapter, we can get a summary of changes and alterations of plant membrane lipids during aging and senescence. As a conclusion, we can say that membrane lipid alteration could be the first sign of senescence and the leading pathway to death, before and after harvest.

The following chapter introduces the hormonal regulation of senescence, ageing, fading and ripening. It also discusses briefly the plant hormones.

Part II deals with characteristics of senescence in special crops.

The first chapter in this part discusses post-harvest physiology of seeds, as related to quality and germinability, the second one the physiology and storage of bulbs: concepts and nature of dormancy in bulbs, and the third one the formation of enzymatic products in fruits during growth and storage.

In Part III the pathological aspects of post harvest storage gets into the focus.

The first chapter deals with the host-pathogen interactions in post-harvest diseases. The most important question is the reduction of the post-harvest deterioration by increasing the resistance of host, controlling of temperature, relative humidity, inert atmospheres, using senescence-inhibiting compounds, etc. The following paper describes the control of post-harvest diseases with antimicrobial agents. The major thrust of current research in post-harvest pathology should be directed towards the development of existing fungicides into practical and economical treatments for reduction of crop losses during storage.

The next review is concerned with the study of hydroxyproline-rich glycoproteins in the cell wall of diseased plants as a defense mechanism. The cell wall really actively participates in the defense of plants through the accumulation of hydroxyprolin-rich glycoprotein.

The chapter entitled "Stress metabolits" introduces the chemical nature and distribution of these metabolites, mechanism of elicitor response-biotic elicitors; abiotic elicitors and toxicity of the stress metabolites.

The last study in this part is "Mycotoxins as a deteriorating factors in stored crops". It deals with four mycotoxins, their chemical nature, their formation and occurrence in foodstuff.

Part IV discusses "Manipulation of the pre- and post-harvest environment to influence quality" which is a very important problem associated with human being.

The first paper deals with hormonal and chemical pre-harvest treatments which influence post-harvest quality, maturity and storeability of fruits.

The following chapter deals with the effect of post-harvest treatments of growth and bioregulators on the quality and longevity of fruits and vegetables. Attention is paid to growth substances and other chemical compounds that have a pronounced effect on the storage life of fresh fruits and vegetables. The manipulation of post-harvest atmosphere for preservation of food crops is described in the next chapter.

Then, results obtained on metabolism, heat transfer and water loss obtained on metabolism, heat transfer and water loss under hypobaric and atmospheric conditions are summarized.

The subsequent chapter presents the results of investigations on maintaining nutritional and processing quality in grain crops during handling, storage and transportation.

The following paper gives an overview of studies on the post-harvest treatment of horticultural produce and developments to maintain quality and preventation damage in western Europe with special reference to the Netherlands.

In the study "Post-harvest quality maintenance of fruits and vegetables in developing countries", factors influencing quality and its maintanence after harvest are discussed.

The following paper deals with a very important question: How is it possible to measure the composition of a product and by which way can be used there information to indicate quality? Instrumental techniques for the qualification of agricultural crops are presented.

Part V discusses the economic aspects of post-harvest losses in the developing world where there is the most urgent need to increase food availability.

The first chapter deals with the post-harvest losses in perishable foods of the developing world, the second one with the solving of the third world food problem and the closing paper discusses the utilization of agricultura wastes, considering some global problems.

The book is supplemented with many figures and tables, and provides a broad spectrum of current basic and practical information on post harvest technology and crop preservation. It may be highly recommended to those interested in the problems and their solition in post-harvest of crops and crop preservation.

Z. Tuba

G. Fekete (ed.): Problems of Coenological Succession, a recension and some comments by E. Kovács-Láng. Akadémiai Kiadó, Budapest, 1985.

The proceedings of a symposium on succession, sponsored by the Ecological and Botanical Institute of the Hungarian Academy of Sciences and held in September, 1982, in Vácrátót, were published at the end of 1985. The editor of the book was co-chairman with A. Borhidi and the chief organizer of the conference. The volume contains 10 papers and the closing remark of the editor summarizing and commenting on the discussions.

It is unnecessary to emphasize the timeliness of the topic; hundreds of papers and books appeared in the past decade in this subject, and there are many research teams dealing with succession all over the world. In Hungary, problems of succession also receive the attention of many scientists; they are motivated by Kerner's tradition, the influence of Soó's phytosociological school and a practical factor, the urgent need of studying degradation processes. The conference was attented by all those interested in giving a talk or simply asking questions on the state-of-the-art.

The first point to be made is that the papers reflect pretty well the heterogeneity of participants in age and scientific interest. It was not an exclusive meeting of botanists. Zoologists, hydrobiologists, and representatives of other areas also attempted to exchange views in terms of a general ecology. The "older" generation, which used classical terms, was faced with the less experienced but demanding "new wave" of younger researchers.

The book gives an overview on ideas and concepts currently attracting the attention of Hungarian students of succession, and informs the reader about new results, problems, difficulties, perspectives and future possibilities of recent research projects.

The second aspect is that the participants agreed to construct a conceptual basis, following an extensive exchange of information and the raise of new questions, to promote the development of a general theory of succession.

Thirdly, the need for a new approach has to be emphasized. In this approach, largely neglected in similar proceedings, the topic of succession is treated in a unified syndynamical

framework. This approach was introduced by P. JUHÁSZ-NAGY and the discussions were successfully kept by G. FEKETE, within the conceptual framework.

What are the most progressive elements of the new approach, as suggested by the papers? The need for a unified syndynamical concept, strongly emphasized by the book, is obviously a long-lasting motivation for future studies.

- The conditions for such a work are the development of operative conceptual constructions, the introduction of new terms and the re-interpretation of existing terminology.
- The importance of dynamic generalizations has to be emphasized. Spatio-temporal processes should receive emphasis in the context of transformations. The generalization of "isolatum" dynamics is necessary.
- The interpretation of the control and regulation of successional processes.
- There is a need for the development and application of an appropriate system of models to study, for example, the problems of stability.

Since the papers are written in Hungarian, a detailed overview of the contents seems unavoidable. The book includes the following titles:

A. BORHIDI: Preface.
P. JUHÁSZ-NAGY: Introduction into syndynamics
G. FEKETE: Succession of terrestrial vegetation: theories, models, reality
A. BORHIDI: Connection between the development of soil and vegetation in tropical succession
I. KÁRPÁTI: Connection of succession of geomorphology and vegetation in flood plains
J. PADISÁK: Succession of phytoplankton
L. VÖRÖS and N. KISS: Seasonal periodicity of phytoplankton and its correlation with eutrophycation. Review and a case study on Lake Balaton
L. GALLÉ: Some peculiarities of the succession in animal communities
K. BÁBA: On the succession of snail communities
K. SZLÁVECZ: Organization and succession of communities on marine rocky shores
B. TÓTHMÉRÉSZ: Stability models in succession research
G. FEKETE: Epilogue

The title of the leading article shows that P. JUHÁSZ-NAGY wishes to examine and interpret succession within a general syndynamical framework. In the spirit of a general ecology, he calls for the construction of a unified conceptual basis, the operative definition of dynamical terms of synbiology, and for finding their relationships and possibilities for their mutual interpretation.

JUHÁSZ-NAGY asserts that the topic of syndynamics includes much more than succession. Syndynamics is the theory of coexistential processes. The subject of syndynamical research is the change of coexistence structures and patterns, studied in most cases as transformations of states.

The formation of an overall, coherent syndynamical conceptual framework is an urgent task, but our recent knowledge is full of wide gaps, and the relevant methodology is insufficient. This is the very reason that every effort has to be made to improve the tools and to find the unified concept.

The history of succession studies tells us that early biocoenology was separated from population dynamics, thus preventing the development of a unified theory of succession. As a result, a suitable connection between their respective representations is still missing in most cases.

The pioneers of general ecology have attempted a sort of unification, with less success. According to JUHÁSZ-NAGY, any advance in this regard could be achieved by a really ecological approach to production biological processes; that is, an appropriate re-interpretation of the terms concerning "limitation — being limited".

What is JUHÁSZ-NAGY's view on the treatment of succession in a general syndynamical framework ? The possible and necessary interpretations he gives originate from simultaneism. His definitions are operative, since they show future research directions, and things to do with these definitions are also explained. Their sequence corresponds with some historical stages, starting from the synphenobiological phenomena to the interpretative role of subdisciplines — population biology, evolutionary ecology, theoretical ecology — through the necessity for the analysis of background ecological processes. In this way, succession research will find its place in syndynamics as a whole. The brief presentation of problems is as follows:
1. Succession is a kind of synmorphogenesis, manifested as the spatio-temporal transformation of certain coenostates. Problems to be examined are:

- — characteristics of coenostates, as special compositional stages, and their representation in phase space;
- — when and under what conditions will coenostates correspond with "classical" terms, such as phase, stage, etc ?
- — characteristics of stochastic transformations ergodicity, markovity, stationarity;
- — the obligate, non-stochastic, character of transformations;
- — relationships between cyclic seasonal changes and succession.

2. Succession is an indicator process, to which ecogenesis, an indicandum (background) process of interpretative role has to be paired. Through ecogenesis, there is a successive rearrangement of tolerance-environment relations.

Problems to be examined include:

- — how ecogenesis is represented, for example, by niche or ecotope transformations ?
- — methods to find correspondence between coenokline and ecoklin (a true environmental gradient);
- — how the "gradient method" may be improved using, say, diffusion models ?
- — what evidence is provided by "macroscopic abrupt events" to reveal ecogenesis ?

3. Succession is one of the syndynamical processes whose better understanding is possible in terms of its relationships to other syndynamical processes (e.g. isolatum dynamics, coevolution).

Problems to be examined are:

- — the interpretative role of population dynamic processes;
- — bionomic strategies of populations, their genetic control and possible relationships to biotic succession;
- — secular succession; what is the mutual interpretability of the dynamics of isolates in a general sense and the evolution of communities;
- — how to study the relationship between "global" and "local" processes in the evolution of the biosphere ?

4. Succession is an organized process, whose better description requires the analysis of "organizational relations" (e.g., complexity, stability) by models of control theory.

Problems to be examined are:

- — how to interpret control, regulation and "being controlled" ?
- — the characteristics of stability and steady state in syndynamical systems, with emphasis on "singularity possibilities" and structural stability;
- — the interpretative role of robust stability;
- — the interpretation of generalized "allocation" problems in the discussion of the "canalization" of synmorphogenesis;
- — extremely important possibilities and limitations of practical questions (especially controllability).

The link among the problems listed above has to be found wherever possible, and their mutual interpretability is also sought.

To develop a modern approach to succession, we should go back to the classics. Since succession is a spatio-temporal process, WATT's (1947) concepts on "pattern and process" should be modernized and improved. In this concept, succession is viewed as a case of synmorphogenesis. In the study of the "canalization" of this synmorphogenesis, the issue of stability is extremely important.

The communities are heterogeneous in their dynamics; this is manifested in the multitude of patterns simultaneously existing and changing with various rates. These patterns may be characterized by basic phenomena (diversity, similarity, and preference) and by their transformation in both space and time. The hypothesis of organized correspondence between patterns and processes may represent the starting point towards the analysis of interacting mechanisms and operativization. However, no advance is possible without the introduction and successive refinement of several new terms and methodological concepts.

In the other opening paper, G. FEKETE presents a review on studies of succession in terrestrial communities, based on the central European (Zürich–Montpellier) and Hungarian (SOÓ–ZÓLYOMI) tradition and published works of the past two decades. Emphasis is laid on theories and suitable models, and their validity is illustrated by case studies and a rich collection of references (87 items).

The discussion, in accordance with JUHÁSZ-NAGY's introduction, is embedded in a general syndynamical framework. Succession is considered as a case of community dynamics.

First, some interesting problems associated with succession research are presented, for example:

— how deterministic is community development?
— is there stable terminal point?
— is succession convergent or divergent?
— the itssue of successional stages, and
— types of succession (primary versus secondary, reversible versus irreversible, allogene versus autogene).

The need for a typology of succession is emphasized.

Of the reasons rendering the development of a unified succession theory difficult, the differences among objects and among methods of succession surveys, and the diverging conclusions arising from these studies are mentioned. The organized succession studies launched recently (FALINSKI, 1977), VAN DER MAAREL (1980, 1981) are promising in this regard.

Then, the paper illuminates some current, rapidly developing areas of vegetation dynamics, grouped into four main topics:

1. historical aspects, development of "verbal" theories,
2. some problems of successional mechanisms,
3. explicit presentation of some models,
4. the background of succession.

1. Regarding historical aspects, (see GOLLEY, 1977) first the fundamental and basic processes in CLEMENTS' succession theory are discussed, together with its influence on the European coenological schools. Then, GLEASON's individualistic concept and the non-Clementsian reinterpretation of succession theory in the 60s are summarized. FEKETE recalls the review in the '70s on the generalization of the deterministic concept of the "controlled" communities. He emphasizes the need for a more comprehensive theory, as expressed in general ecology. The three alternative verbal models suggested by CONNELL and SLATYER (1977) (facilitation, inhibition, and tolerance) are explained not neglecting the fact that these authors call our attention to competition and other interactions between populations.
2. In the second part, some characteristics of successional phenomena and events, and some basic questions regarding the mechanism of succession are discussed. The scale-dependence of succession in both time and space is emphasized; it has to be considered when interpreting successional processes, e.g. when finding analogy between terrestrial and planktonic processes (relationship between life cycles and environmental fluctuations). Some effects of the duration of succession, the relationship between duration and number of species; the known characteristics of colonization are demonstrated and then reference is made to a possible recursive property of succession.
3. The presentation of models includes two groups of processes (deterministic versus stochastic), with special attention to MARKOV models.

The deterministic linear differential equations have applications to the description of forest succession. The series of papers by van HULST (1979a, b, 1980) is a significant step in eliminating the wide gap between theories and models. As examples, FEKETE interprests two models of van HULST (1979a), which are based on population dynamics.

As to the application of MARKOV models, succession is interpreted as a stochastic process following MACARTHUR (1958, 1961). The matrix representation, characteristics, applicability and tractability of MARKOV models are discussed. Since the theory of finite MARKOV chains is quite elaborated, MARKOV models offer attractive and often adequate tools for the description and simulation of vegetation dynamics and for testing verbal models of succession. The main motivation in their application is that information is obtained on the equilibrium state and that the type and duration are both determined as the coenosystem converges towards equilibrium. A prerequisite to its application is that vegetation development is assumed to be convergent. The paper refers to some successful applications of the models in simulating forest development (replacement of tree species), for which HORN gives the best examples, and also in describing vegetation dynamics of grasslands.

Then, possibilities for the formalization of some partly verbal models (facilitation, cyclic, tolerance, inhibitive, chronic patchy disturbance, "quasi-realistic") are outlined, showing the validity limits of existing models. The type of transitional matrices is determined by interspecific relationships, and the dynamics, adaptive strategies and other, the so-called

vital, attributes of populations. The paper informs us on realistic cases and on the consequences of simulations starting from hypothetical situations. Then, difficulties with the application and some limitations of MARKOV models are pointed out. These are:

— how general is convergence in vegetation development?
— is markovity valid for plant communities?

Some evidence seem to be contradictory with these statements.

4. Regarding the background of succession, the paper analyses the role of certain characteristics of populations and the connection between succession and ecogenesis (the ecological background process). Examples demonstrate the significance of reproductive potential and the strategies; the reproductive characteristics. Based on results of his own surveys, he demonstrates the dependence of reproductive allocation on physical stress and competition, and the role of reproductive allocation in the adaptation and population dynamics of sand steppe vegetation.

When interpreting background processes of succession, we are faced with a multitide of process-groups that are mutually regulated, but their examination is possible only one by one.

FEKETE emphasizes the role of illumination pattern in the regeneration cycle. This pattern, as a driving structure, influences the "light hierarchy" of populations and the processes of reinvasion. The control and the temporal coordination of controlling and regulating processes in the ecosystem are linked to this structure. The changes of pattern and the background processes evoke the evolution of niche space and lead to the establishment of new species. Niche overlap and breadth are subject to change, and in mature communities a niche divergence develops as a result of competitive effects of the past.

The change of niche is related to the physiological properties of populations. Thus, the ecophysiology of succession is an important developing interdisciplinary subject, as examplified by the studies of BAZZAZ (1979) and co-workers.

FEKETE's paper gives an impressively broad overview on our knowledge on the mechanisms and models of terrestrial coenological succession. Theory and reality are contrasted with each other so as to motivate the reader for further contemplation and deliberation, and to stimulate advancement in succession research.

As one of his results in tropical studies, A. BORHIDI presents a successional series of vegetation and soil, which is the most typical on the limestones of Cuba. In this evolutionary process of large temporal scale, the characteristics of a biotic and secular succession well-distinguishable in the temperate zone are both recognized.

The states of soil development distinguished according to the degree of latosolization, and the processes of silicate transformation and degradation during soil genesis are compared with successional stages in the vegetation, delimited by structural and biomass properties. His experience suggests that the monoclimax concept is not valid under tropical conditions, since the climax formations and soil types locally differ depending on the amount of precipitation and also on parent material.

I. KÁRPÁTI presents a broad overview on the geomorphology and vegetation succession in the floodplain of major rivers of Hungary (Danube, Tisza, Drava) based on experience of a long research project and literature sources. His method is mostly indirect, temporal events are deduced from spatial changes. The study of pattern and its change in the floodplain vegetation is important from both practical and theoretical viewpoints. During construction work (e.g. river regulation, construction of hydroelectric stations and storage lakes) the water table in the soil, which primarily determines pattern and process, is often changed.

In these cases, the zonation of vegetation in the floodplain is "deterministic", facilitating the prediction of succession from water level changes. At the same time, the mechanisms and the speed of successional processes may and should be examined.

J. PADISÁK presents a review on the main results and terminological problems of studies on phytoplankton succession. Emphasis is placed on shallow lakes of the temperate zone. Results of case studies illustrate the relevance of general concepts to specific problems of phytoplankton research. By discussing the succession of phytoplankton, this paper attempts to eliminate the terminological discrepancy between terrestrial vegetation studies and phytoplankton surveys.

The dynamics of phytoplankton is interpreted within the framework of general ecology and the discussion concernes many little-known areas. Some problems mentioned are not restricted to phytoplankton; they are general dissues of succession theory. However, certain questions are specific to phytoplankton communities. Evaluating the "nature" of phytoplankton, the author emphasizes that the life-span of alga species varies in a broad interval

and is much shorter than in the terrestrial plants. The lifespan is short relative to the time-scale of great abiotic changes (e.g. climate, weather), therefore different scaling becomes necessary. Further difference is that phytoplankton exists only in water, thus it is "azonal", and the term "climax" used in the description of terrestrial succession does not apply.

In phytoplankton communities, morphological and especially genetical and physiological diversity is high. Although they are less co-ordinated and more ambiguously defined than the terrestrial communities, their organized status is proved by the existence of co-ordination, the ability to occur repetitively, the resistence to the establishment of alien elements, and some stability against perturbation effects.

Succession and other temporal changes (fluctuation, periodicity) are interpreted in algology showing that published papers consider succession only as a temporal process. However, succession should be interpreted as a spatio-temporal process, as shown by case studies performed in Lake Fertő and Lake Balaton.

There is much emphasis on the seasonal dynamics and its interpretation in the phytoplankton communities of the temperate zone. The seasonal changes of spatio-temporal pattern of phytoplankton are considered succession, as a directed pattern transformation at a small temporal scale, as distinguished from the cyclic succession observed in tropical lakes and from fluctuations of phytoplankton.

The problem of directed succession of phytoplankton is an exciting topic in the paper. Whereas the direction of seasonal succession is generally accepted as being evident in the lakes of the temperate zone; direction of succession on a longer time scale is almost exclusively confined to the problem of eutrophication. During a long eutrophication process the two directions are combined leading to a hierarchical directionality. Its interpretation, as emphasized by the author, is not possible without an appropriate model repertoire. The existence of directed succession on the long time-scale, which is not connected to eutrophication, remains an open question as long as case studies are not available.

The description and prediction of succession of phytoplankton and, in general, of limnic communities would be helpful in solving several practical problems. However, our knowledge is insufficient to achieve any advance in this regard.

A case study by L. Vörös and N. Kiss analyzes the seasonal periodicity of the phytoplankton in three basins of Lake Balaton which are in various stages of eutrophication. According to the cluster analysis of plankton pattern based on species composition, abundance, biomass, surface/volume ratio, and the percentage contribution of taxa to the total biomass, five seasonal periods were distinguished; they correspond to the concept of "three-phase succession" introduced by Margalef (1960). According to the experience of the authors, eutrophication changes the direction of seasonal succession, usually backwards, but sometimes the diversity peaks may indicate the occurrence of new coenoses as well.

L. Gallé discusses two topics of succession in animal communities.

First, considering succession as some process of stabilization, some features of food webs are examined which are important as to the stability characteristics of chains and webs. Terrestrial food chains selected from the literature are ordered according to successional stages (pioneer, grassland stage, forest margin-grove, and forest). The length and diversity of relations in food webs are analyzed together with the compartmentalization of food webs and the specialization of predators.

Regarding trophic chains and competitive mechanisms, the author concludes that the complexity of tr ophic webs decreases as succession proceeds; the compartmentalization of webs is uncorrelated with complexity and has a maximum during succession, decreasing towards the climax (forest) stage. Along succession, the average specialization of predators increases, whereas there is no defined trend as to the "predator-specialization" of prey populations. These facts support the view that in a trophic system succession is associated with a stabilization process. A contraindication is that the length of trophic chains calculated as the similarity between the rows and columns of the trophic webs does not follow a well-defined trend in the successional processes examined.

In the second part of the paper, competitive interactions and changes of the niche space are demonstrated by a study of *Formicidae* ants in the successional sere of sand grasslands. During this succession, the diversity of ant fauna has a maximum, since in the second part of succession the relatively frequency of more successful competitors increases, leading to the decrease of opportunist competitors. There is a multiple rearrangement of niche space for the core and satellite species during succession; during this the niche space utilized by the coalition of species increases in volume.

The case study presented does not support the hypothesis of successional niche specialization but opens new possibilities for the reinterpretation of competition and compositional stability.

K. Bába summarizes his malacological studies performed for 15 years in the Hungarian Great Plain. The snail assemblages from thre esuccessional seres (water effected organogenic and mineralogenic, and a sandy) of vegetation are analyzed for quantitative and qualitative properties. An attempt is made to reconstruct successional processes of snail assemblages. The investigation of interspecific associations of snails, and of the change of species composition and abundance over the modification of abiotic factors shows that the succession of snail assemblages follows the vegetational changes in the communities examined and is limited mainly by humidity conditions.

The environmental parameters show the increasing trend in the subsequent stages, as supposed by Odum (1969).

The analysis of pathways of possible successional directions suggests that the stages, which correspond to the subassociations in vegetation, are manifested in mosaics that exist simultaneously. Culture effects (sylviculture) cause strong structural simplification and depauperization of the fauna.

K. Szlávecz reports on the objectives, results and conclusions of the marine ecological investigations conducted by J. Connell and co-workers in the area of Ellwood Beach Sousa (1979, 1980). These studies attempt to reveal the mechanism of succession in the intertidal and sublitoral zone. The validity of verbal models is tested and analogies with terrestrial successional processes are found, so much the more because a common property of intertidal and terrestrial communities is the dominance of sessile organisms. The studies of the "Santa Barbara" group emphasize both the different tolerance of colonizing species against physical environment and the selective herbivory and predation which facilitate the establishment of new species. The influence of latter factors has been largely neglected in studies of terrestrial succession. Experience suggests that the community is found locally in various successional stages, thanks to dynamic heterogeneity and physical disturbance, and its development cannot be described by a single model. Stability has not only a temporal aspect, as maintenance against permanent perturbation is a much more crucial problem.

The short paper by B. Tóthmérész outlines the role of stability models in succession research. The author's approach to succession study is presented in a population biological framework. Perspectives of establishing a unified methodology are discussed as a contribution to P. Juhász-Nagy's introductory notes. The properties and the usefulness of mathematical models of stability are presented together with possibilities for the interpretation of stability types (orbital, structural), with special emphasis on singularity. The behaviour of non-linear models that are capable of describing synbiological systems are analyzed. "Stability behaviour" and the interpretation of "catastrophe" are demonstrated using a potential function. These models can be used in succession research to examine niche segregation and the alternative successional pathways of degradation.

For successional studies at the population level, the author emphasizes the importance of a non-linear generalization of allometric relationships, which may help in the description of competition and allelopathic relationships (e.g. Antonelli 1980), from an allometric approach towards synallometry. In this context, the generalized stochastic canalization concept of climax is outlined following Waddington (1957).

The actuality of the volume lies in the fact that syndynamics is becoming more and more important and even indispensable from both practical and theoretical viewpoints. The explicit intention of authors was to stimulate syndynamical research in Hungary. Fortunately, some publications are already available in this subject reporting on new methods and results. Examples not presented in the book will complete our picture on the recent state of syndynamical research in Hungary:

Juhász-Nagy developed a family of methods, based on a fundamentally new coenological conceptual system, for the description of successional and degradation processes using information statistics (Juhász-Nagy 1972, 1973, 1980; Juhász-Nagy and Podani 1983). Précsényi (1981) analyzedthe species/individual diversity of sand vegetation along a complete successional sere. Virágh (1982) used permanent plots to examine structural changes during degradation and secondary succession in grasslands treated by various herbicides.

In the pioneer stages of succession, the population biological aspect is to be emphasized. Bartha (in Szegi et al, 1988) analyzed the structure and organization of primary succession on a refuse dump. Fekete and Melkó (1981) showed that reproductive allocation in terms of population dynamics and demography is under different control in the subsequent stages of succession in sand vegetation. Also, the photosynthetic production of the populations of dominant species changes as the community is reorganized (Fekete and Tuba 1982).

The volume is unique in the sense that very few books discuss on the same theoretical grounds the succession of plant and animal communities. (As positive example, it should be mentioned the excellent compilation edited by Gray, Crawley and Edwards, 1987 con-

taining the papers of the 26th Symposium of the British Ecological Society, 1984, hence held two years later then ours.) In summary, the volume presents a useful up-to-date review on the state-of-the-art by showing many interesting results and raising unsolved difficult questions. Its special advantage is that the conceptual basis first published here, and the existing principles and useful models plus the case studies represent a good material to promote the development of a more general succession theory, to show future possibilities and practical and theoretical potentials.

REFERENCES

Antonelli, P. L. 1980: Optimal growth of an ideal coral reef. Acta Cientia Venezolana **31:** 521—525.

Bazzaz, F. A. 1979: The physiological ecology of plant succession. Ann. Rev. Ecol. Syst. 10: 351—371.

Connell, J. H., Slatyer, R. O. 1977: Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. **111:** 1119—1144.

Falinski, J. B. (ed.) 1977: Vegetation Dynamics. Phytocoenosis 7.

Fekete, G., Melkó, E. 1981: Reproductive allocation in the stages of sandy succession. Acta Bot. Acad. Sci. Hung. **27:** 351—364.

Fekete, G., Tuba, Z. 1982: Photosynthetic activity in the stages of sandy succession. Acta Bot. Acad. Sci. Hung. **28:** 291—296.

Golley, F. B. (ed.) 1977: Ecological succession. Benchmark papers in Ecology 5. Dowden, Hutchinson, Ross, Stroudsburg.

Gray, A. J., Crawley, M. J. Ú Edwards, P. J. (eds:) (1987): Colonization, succession and stability. Blackwell Sc. Publications. Oxford.

Horn, H. S. 1975: Markovian properties of forest succession. In: Cody, M. L., Diamond, J. M. (eds.): Ecology and evolution of communities. 196—211. Harvard University Press.

Horn, H. S. 1981: Succession. In: May, R. M. (ed.): Theoretical Ecology Blackwell Sc. Publications. Oxford.

van Hulst, R. 1979a: The dynamics of vegetation: succession in model communities. Vegetatio **39:** 85—96.

van Hulst, R. 1979b: On the dynamics of vegetation: Markov chains as models of succession. Vegetatio **40:** 3—14.

van Hulst, R. 1980: Vegetation dynamics or ecosystem dynamics: dynamic sufficiency in succession theory. Vegetatio **43:** 147—151.

Juhász-Nagy, P. 1972: A növényzet szerkezetvizsgálata: új modellek. I. Bevezetés (The structure of vegetation: new models. I. Introduction) Bot. Közlem. **59:** 1—5.

Juhász-Nagy, P. 1973: A növényzet szerkezetvizsgálata: új modellek. II. Elemi beskálázás a florális diverzitás szerint. (The structure of vegetation: new models. II. Elementary scaling and floral diversity). Bot. Közlem. **60:** 35—41.

Juhász-Nagy, P. 1980: A növényzet szerkezetvizsgálata: új modellek. III. Florális diverzitás: elemek. (The structure of vegetation: new models. III. The properties of floral diversity). Bot. Közlem. 67: 185–193.

Juhász-Nagy, P., Podani, J. 1983: Information theory methods for the study of spatial processes and succession. Vegetatio 51: 129–140.

van der Maarel, E. (ed.) 1980: Advances in Vegetation Science: Succession. Vegetatio 43.

van der Maarel E. et al. (eds) 1981: Vegetation Dynamics. Vegetatio 46/47.

MacArthur, R. H. 1958: A note on stationary age distributions in singlespecies populations and stationary species populations in a community. Ecology 39: 146–147.

MacArthur, R. H. 1961: Community. In: Gray P. (ed.): The encyclopedia of the biological sciences. 262–264. Reinhold, New York.

Margalef, R. 1960: Temporal succession and spatial heterogneity in phytoplankton. In: Buzzati-Traverso, A. A. (ed.): Perspectives in Marine Biology. 329–349. Univ. Calif. Press. Berkeley.

Newman, E. J. (ed.) 1982: The plant community as a working mechanism. Blackwell Sc. Publications. Oxford.

Odum, E. P. 1969: The strategy of ecosystem development. Science 164: 262–270.

Précsényi, I. 1981: Changes in the diversity of vegetation during succession. Acta Bot. Acad. Sci. Hung. 27: 189–199.

Sousa, W. P. 1979: Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Monogr. 49: 227—254.

Sousa, W. P. 1980: The responses of a community to disturbance: The importance of successional age and species life histories. Oecologia (Berl.) 45: 72–81.
Szegi, J., Oláh, J., Fekete, G., Halász, T., Várallyay, Gy. & Bartha, S. 1988: Recultivation of spoil banks disturbed by open cut mining activity in Hungary. Ambio 17: 137–143.
Virágh, K. 1982: Vegetation dynamics induced by some herbicides in a perennial grassland community I. Acta Bot. Acad. Sci. Hung. 28: 427–447.
Waddington, C. H. 1957: The strategy of Genes. Allen and Unwin, London.
Watt, A. 1947: Pattern and process in the plant community. J. Ecol. 35: 1–22.

Jakucs, P. (ed.): Ecology of an Oak Forest in Hungary. Results of "Síkfőkút Project" 1. Akadémiai Kiadó, Budapest, 1985, 546 pp.

The "Síkfőkút Project" research programme — which is a Hungarian contribution to the UNESCO-MAB programme — was initiated by the Institute of Botany (later: Institute of Ecology) of the Kossuth L. University, Debrecen, with the leadership of prof. P. Jakucs, member of the Hungarian Academy of Sciences. This volume summarizes the results concerning the structure and functioning of the autotrophic components of the oak forest (*Quercetum petraeae-cerris*) studied. The number of contributors is 21. The book consists of nine large chapters.

Chapter 1 discusses the aims and preparation of the research. P. Jakucs gives an overview on the topics and organization of the investigations.

In Chapter 2, information is given on the landscape of which the study area is a part (short description of the geomorphology, soils, climate; of man's influence).

The phytosociological characterization of the stand studied is given in Chapter 3, as well as the description of life form distribution, flora elements, and the distribution of the so-called indicator numbers (concerning the temperature, water regime, soil acidity) of the species. The description of soil conditions is followed by a richly documented description of weather conditions (main meteorological data between 1973–1978), radiation conditions above and inside the stand, radiation interception, distribution of the temperature in the forest. The huge amounts of data were obtained by a digital data collector measuring network.

Under structure of the forest (Chapter 4) various ones: spatial and time-structures are meant, either of physiognomic (visible) or of abstract characters. There are documented and explained properties such as; the number of species and individuals, height, trunk diameter and distribution of their values, stem distance, cover, and leaf number. For the estimation of assimilation area, 15 trees ("average individuals") were cut and the leaves counted. Total LAI in the whole forest is 8.28 (6.58 of the tree level, 1.44 of the shrubs, 0.26 of the herb layer). The phenology of two tree species, five shrubs, and ten herb species was followed in five consecutive years. An interesting special contribution to this chapter is a study of algae living in the forest soil.

Estimations for total phytomass and primary organic matter production are to be considered as important aims of the book (Chapter 5). In case of woody plants, regression estimates based on allometric relations are used. To the herbs, both the harvest method and the individual sampling method were applied. The total phytomass of the forest was 248 t/ha, of this 97.1% falls to the tree layer, 2.6 to the shrubs and 0.3 to the herb layer. The above-ground part makes up for 85.5% the total assimilating fraction 2.25% of the total phytomass. It was stated that of the primary net production 84% falls to the tree layer, 13% to the shrubs. Comparing phytomass and production, the amount of the annual organic matter production was more than 5% of the total phytomass.

Chapter 6 refers not only to structure but to the functioning of the forest. This is valid first of all to the paper on leaf growth of trees. Area and weight changes of light- and shade-adapted leaves of *Quercus petraea* and *Qu. cerris* are given. In one-year old shoots standard growth analyses were carried out, parallel in "light layers" and "shade layers" and so information was given on the assimilation capacity and morphological development of the photosynthetic system of the two oak species for three years. These investigations are to be regarded of pioneering importance, both in methodical and practical respects. Again, a structural property is discussed in a survey on photosynthetic pigment distribution, here the vertical and seasonal changes are described. It can be regarded as an important new approach analysing the so-called mixed (multispecies) samples. It revealed by comparing the data with those concerning only one species the supraindividual pigment homogeneity, first of all in the herb layer.

Chapter 7 deals with the energy content of the dominant autotrophs and their components, and discusses variations between years, seasons, etc. The energy flow through the forest plants and the ecological efficiency are also evaluated.

Chapters 8 and 9 are devoted to the elemental composition. Chapter 8 can be considered as more static, the latter as a more dynamic one. Chapter 8 discusses the results on the concentration of nutrients (carbon, nitrogen, potassium, phosphorus, calcium, magnesium, iron, manganese, copper, zinc, sodium) in trees and herb species, and analyses connections between nutrients and phytomass, and seasonal variation. A special and important evaluation of the results is given from time-dynamical point of view: high turnover rates of iron, potassium and sodium are indicated, whereas the rates of N and P are the lowest (aboveground parts). The turnover rates estimated for different years deviate markedly.

In Chapter 9 the results concerning the element migration and litter decomposition are demonstrated and discussed. The amount and element content of precipitation are evaluated in a very circumstantial manner, throughfall and also stemflow, minerals reaching the soil with precipitation are analysed. It had been shown that the connection between the amount of precipitation and its elemental concentrations can be best expressed by a power function. The exmination of litter decomposition and its rate was done with a many-sided approach. Field experiments were carried out with litter bags, and the following questions were answered: What is the decomposition rate of the most important species ? Do the leaves of the species studied influence the decomposition rates of other species ? What is the bacterial and fungi number, and the hyphal activity in the course of decomposition ? How does the element content of litter change in the course of decomposition ? The dynamics of elements in the soil (seepage fluxes and their element concentration) were also discussed.

Finally, prof. JAKUCS gives a conclusive summary, concerning mainly the results discussed in Chapters 8 and 9. So we get a good picture on the balance of some elements in the ecosystem and on the quantities in certain compartments (10 compartments had been distinguished). Trends and temporal changes in element circulation in the intrasystem cycles are also given.

Special parts are devoted to the problem of soil acidity. The leaching tendency of Ca and Mg cations has been shown. This fact can be regarded — according the opinion of the author — as analogous to the soil acidification processes. As a result of acidifying agents (nitrogen compounds getting into the forest from intensive fertilization of larger agricultural areas, sulphur compounds as air pollution factors), the Mg and Ca cations can easily be washed out with the seepage of the ecosystem and can get into the deeper soil layers. The other conclusion concerns the carbon cycle. A huge quantity of carbon atoms can find their way into the soil-surface layers of the ecosystem from the CO_2 of the atmosphere, they may link with Ca and Mg ions. Their streaming downward mostly takes place in the form of hydrocarbonate and they either increase the hydrocarbonate content of groundwater or become bound to the soil colloids. At last, the CO_2 surplus of the atmosphere, caused by rapidly increasing industrialization, will be bound in form of secondary dolomite or limestone.

The documentation and illustration of the papers are rich. The evaluation of the results is supported by various mathematical analyses and by considering the ample, carefully selected, up-to date literature. It is a well-edited book.

The work gives us the first, many-sided, detailed and comprehensive description of the structural and functional characteristics of the zonal turkey oak-oakwoods widely distributed in north-Balkan and Pannonian landscapes. It represents well the scientific activity of the professorship and the accompanying research groups. At the same time, it also gives a characteristic picture on the developmental status of Hungarian experimental ecology.

We expect with much interest the further volumes concerning the results of "Síkfőkút Project" (the results relating to the heterotrophic level, the syntheses in forms of various models, practical evaluations, etc.) to appear.

G. FEKETE

AKADÉMIAI KIADÓ presents

a new volume in the series

NATURAL HISTORY OF THE NATIONAL PARKS IN HUNGARY

THE FAUNA OF THE KISKUNSÁG NATIONAL PARK

[Volume 2]

edited by S. Mahunka

In the Carpathian Basin the Kiskunság National Park is situated in the center of the Hungarian Great Plain. This National Park is inhabited by a unique fauna which has partly become extinct anywhere else in Central Europe. Highly varied biotopes like the saline puszta, the sand dunes, Juniper woodlands, inundation groves and a number of marshes provide their habitat.

The field works lasted for four years. The collected material was evaluated by an international team of scientists. The taxonomic, zoogeographic and ecological results have revealed many new surprising features of interdependence.

Besides the documentation of the natural gene bank protected here, the obtained data will hopefully inspire further comparative zoogeographical and ecological studies.

Prospective readership: zoologists, ecologists

1987. 479 pages. Neumerous illustrations

Hardbound. $ 55.00

ISBN 963 05 4352 4

AVAILABLE through your bookseller or our General Distributors:

K U L T U R A

Hungarian Foreign Trading Company

P. O. B. 149

H–1389 BUDAPEST, Hungary

The papers generally have the following components, which should be presented in the order listed:

1. Title, name of the author(s), affiliation, dataline, abstract, keywords
2. Text, acknowledgements
3. References
4. Footnotes
5. Tables
6. Figure captions
7. Illustrations

1. The *affiliation* should be as concise as possible and should include the complete mailing address of the authors. The date of receipt of the manuscript will be supplied by the editors. The abstract should be in English and should not exceed 250 words. It should clearly and simply summarize the most important methods and results. 5–10 significant expressions describing the content are used as keywords. Authors may recommend these keywords.

2. The *text* of the papers should be of high stylistic standard, requiring minor corrections only. The section headings, names of authors cited, latin names and terms should *not* be underlined or in capitals. Quantities should be expressed in SI-units.

3. *References* are accepted only in the Harvard system. Citation in the text must be as:
... (Jakucs 1961) ... or Jakucs (1961) ...
... (Fekete and Précsényi 1981) ...
... (Borhidi et al. 1979*a*) ...

The list of references should contain the names and initials of all authors (the abbreviation et al. is not accepted here); for *journal articles* year of publication, the title of the paper, title of the journal abbreviated, volume number, first and last pages.

For *books* or *chapters in books*, the title is followed by the publisher and place of publication. Book title words should be written with majuscules. Titles of papers published only in Hungarian should be translated in parentheses. All items are recommended to be cited both in the text and references.

Examples:

Jakucs, P. 1961: Die Phytozönologischen Verhältnisse der Flaumeichen-Buschwälder Südostmitteleuropas. Akadémiai Kiadó, Budapest.
Fekete, G., Précsényi, I. 1981: Niche structure of a perennial sandy grassland. In: Stefanovits, P., Berczik, Á., Fekete, G., Seidl, M. (eds): Man and the Biosphere Programme. Survey of 10 Years Activity in Hungary. Budapest, 68–102.
Borhidi, A., Muñiz, O., Del Risco, E. 1979*a*: Clasificación fitocenologica de la vegetación de Cuba. Acta Bot. Hung. **25**: 263–301.
Jakucs, P. 1973: „Síkfőkút Projekt". Egy tölgyes ökoszisztéma környezetbiológiai kutatása a bioszféra program keretein belül. (Síkfőkút-Project. Environmental-biological research of an oakwood ecosystem within the framework of the Biosphere program). MTA Biol. Oszt. Közl. **16**: 11–25.

4. *Footnotes* should be typed on a separate sheet.

5. *Tables* should be typed on separate pages. They should be numbered serially with arabic numerals and have a concise heading each. Vertical lines are not used. Clear wording of column heads is advisable.

6. *Figure captions* should de provided on a separate sheet.

7. *Illustrations* must not be inserted in the text. Figures will be redrawn. Therefore the most important point is the clearness of the figures, even pencil drawings are accepted (with a duplicate). Photographs should be sharp and well contrasted. All the illustrations should bear the figure number and author's name in pencil on the reverse.

*

The editors will send information to the first author about the arrival and *acceptance* of the paper. Two *proofs* will be provided, which are requested to be returned within 48 hours of receipt to the editor. Alterations in the text and especially in the illustrations are expensive and should be avoided. Hundred *offprints* are supplied free of charge.

These instructions are valid as from 1983.

Periodicals of the Hungarian Academy of Sciences are obtainable at the following addresses:

AUSTRALIA
C.B.D. LIBRARY AND SUBSCRIPTION SERVICE
Box 4886, G.P.O., *Sydney N.S.W. 2001*
COSMOS BOOKSHOP, 145 Ackland Street
St. Kilda (Melbourne), Victoria 3182

AUSTRIA
GLOBUS, Höchstädtplatz 3, *1206 Wien XX*

BELGIUM
OFFICE INTERNATIONAL DES PERIODIQUES
Avenue Louise, 485, *1050 Bruxelles*
E. STORY-SCIENTIA P.V.B.A.
P. van Duyseplein 8, *9000 Gent*

BULGARIA
HEMUS, Bulvar Ruszki 6, *Sofia*

CANADA
PANNONIA BOOKS, P.O. Box 1017
Postal Station "B", *Toronto, Ont. M5T 2T8*

CHINA
CNPICOR, Periodical Department, P.O. Box 50
Peking

CZECHOSLOVAKIA
MAD'ARSKA KULTURA, Národni třida 22
115 66 Praha
PNS DOVOZ TISKU, Vinohradská 46, *Praha 2*
PNS DOVOZ TLAČE, *Bratislava 2*

DENMARK
EJNAR MUNKSGAARD, 35, Nørre Søgade
1370 Copenhagen K

FEDERAL REPUBLIC OF GERMANY
KUNST UND WISSEN ERICH BIEBER
Postfach 46, *7000 Stuttgart 1*

FINLAND
AKATEEMINEN KIRJAKAUPPA, P.O. Box 128
00101 Helsinki 10

FRANCE
DAWSON-FRANCE S.A., B.P. 40, *91121 Palaiseau*
OFFICE INTERNATIONAL DE DOCUMENTATION ET LIBRAIRIE, 48 rue Gay-Lussac
75240 Paris, Cedex 05

GERMAN DEMOCRATIC REPUBLIC
HAUS DER UNGARISCHEN KULTUR
Karl Liebknecht-Straße 9, *DDR-102 Berlin*

GREAT BRITAIN
BLACKWELL'S PERIODICALS DIVISION
Hythe Bridge Street, *Oxford OX1 2ET*
BUMPUS, HALDANE AND MAXWELL LTD.
Cowper Works, *Olney, Bucks MK46 4BN*
COLLET'S HOLDINGS LTD., Denington Estate,
Wellingborough, Northants NN8 2QT
WM DAWSON AND SONS LTD., Cannon House
Folkstone, Kent CT19 5EE
H. K. LEWIS AND CO., 136 Gower Street
London WC1E 6BS

GREECE
KOSTARAKIS BROTHERS INTERNATIONAL BOOKSELLERS, 2 Hippokratous Street, *Athens-143*

HOLLAND
FAXON EUROPE, P.O. Box 167
1000 AD Amsterdam
MARTINUS NIJHOFF B. V.
Lange Voorhout 9-11, *Den Haag*
SWETS SUBSCRIPTION SERVICE
P.O. Box 830, 2160 Sz Lisse

INDIA
ALLIED PUBLISHING PVT. LTD.
750 Mount Road, *Madras 600002*
CENTRAL NEWS AGENCY PVT. LTD.
Connaught Circus, *New Delhi 110001*
INTERNATIONAL BOOK HOUSE PVT. LTD.
Madame Cama Road, *Bombay 400039*

ITALY
D. E. A., Via Lima 28, *00198 Roma*
INTERSCIENTIA, Via Mazzé 28, *10149 Torino*
LIBRERIA COMMISSIONARIA SANSONI
Via Lamarmora 45, *50121 Firenze*
SANTO VANASIA, Via M. Macchi 58
20124 Milano

JAPAN
KINOKUNIYA COMPANY LTD.
Journal Department, P.O. Box 55
Chitose, *Tokyo 156*
MARUZEN COMPANY LTD., Book Department
P.O. Box 5050 Tokyo International, *Tokyo 100-31*
NAUKA LTD., Import Department
2-30-19 Minami Ikebukuro, Toshima-ku, *Tokyo 171*

KOREA
CHULPANMUL, *Phenjan*

NORWAY
TANUM-TIDSKRIFT-SENTRALEN A.S.
Karl Johansgata 43, *1000 Oslo*

POLAND
WĘGIERSKI INSTYTUT KULTURY
Marszalkowska 80, *00-517 Warszawa*
CKP I W, ul. Towarowa 28, *00-958 Warszawa*

ROUMANIA
D. E. P., *Bucuresti*
ILEXIM, Calea Grivitei 64-66, *Bucuresti*

SOVIET UNION
SOYUZPECHAT — IMPORT, *Moscow*
and the post offices in each town
MEZHDUNARODNAYA KNIGA, *Moscow G-200*

SPAIN
DIAZ DE SANTOS Lagasca 95, *Madrid 6*

SWEDEN
ESSELTE TIDSKRIFTSCENTRALEN
Box 62, *101 20 Stockholm*

SWITZERLAND
KARGER LIBRI AG, Petersgraben 31, *4011 Basel*

USA
EBSCO SUBSCRIPTION SERVICES
P.O. Box 1943, *Birmingham, Alabama 35201*
F. W. FAXON COMPANY, INC.
15 Southwest Park, *Westwood Mass. 02090*
MAJOR SCIENTIFIC SUBSCRIPTIONS
1851 Diplomat, P.O. Box 819074,
Pallas, Tx. 75381-9074
READ-MORE PUBLICATIONS, INC.
140 Cedar Street, *New York, N. Y. 10006*

YUGOSLAVIA
JUGOSLOVENSKA KNJIGA, Terazije 27, *Beograd*
FORUM, Vojvode Mišića 1, *21000 Novi Sad*

Index: 26.006